WHEN AND WHERE WILL I FIND MY NEXT MEAL?: QUANTIFYING THE EFFECTS OF SPATIOTEMPORAL FORAGE PREDICTABILITY ON UNGULATE MOVEMENT BEHAVIORS IN TWO DISPARATE ECOSYSTEMS

by

Madeline Standen

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science (Environment and Sustainability)
in the University of Michigan
August 2023

Thesis Committee:
Professor Neil H. Carter, Chair
David C. Stoner, PhD
Mark A. Ditmer, PhD

Abstract

Environmental predictability is increasingly accepted as an overarching driver of animal movement strategies, via its role in the evolution of cognitive abilities that allow species to exploit the spatiotemporal variability of their environments. Recent research has furthered our understanding of how predictability not only *underlies* animal movement tactics, but also *directs* movement decisions as a source of information relevant to behaviors such as site fidelity and home-range establishment. Although research has examined the relationship between predictability and movement strategies at the species level, the mediating influence of environmental context is rarely considered. In addition, research has mainly focused on the relationships between predictability and large-scale movement behaviors, and much less is known about environmental predictability in regard to animal movement over finer scales. We address these knowledge gaps by examining how environmental predictability of a mule deer seasonal home ranges relates to average daily movement in two populations inhabiting disparate ecoregions in Utah, USA. We employ two separate metrics of predictability, representing spatial and temporal constancy of Normalized Difference Vegetation Index (NDVI) values, and explored how home range area and forage abundance modulated the relationships between constancy and daily relocation distance. We found that spatial constancy of an individual's home range significantly impacted daily relocation distance during the summer and had significant interactions with home range area and forage availability. Interestingly, individuals inhabiting spatially predictable home ranges moved more when in a seasonally limiting environment, and less in a non-limiting environment, and forage availability within a spatially predictable home range functioned to reduce the directional impacts of predictability. Temporal constancy was a significant predictor of daily movement in non-limiting seasonal environments, resulting in shorter daily movements in temporally predictable home range areas. Finally, I found a significant interaction between spatial and temporal constancy, which resulted in shorter daily movement of individuals inhabiting home ranges that were spatially *and* temporally predictable. Together, our results demonstrate the use of environmental predictability in practical foraging decisions that enable animals in these populations to meet nutritional and life-history requirements and support the need to consider environmental context when studying environmental predictability and animal movement. Understanding how habitat quality and predictability impact daily movements and energy expenditure of ungulates at a population level aids our ability to predict how shifts in vegetation dynamics will impact individual fitness, population demographics, and ecosystem functioning.

Table of Contents

Introduction

Movements are the product of interactions between an animal and its environment (Schick et al., 2008). Environmental predictability – reliability of an area in terms of resource availability – has garnered attention as an overarching driver of movement behavior and large-scale movement tactics of a wide variety of taxa (Bastille-Rousseau et al., 2017, *giant tortoises*; Passadore et al., 2018, *dolphins*; Abrahms et al., 2019, *whales;* Ferguson et al., 1999, *bears*). As an individual's survival depends on its ability to locate resources, environmental predictability provides fitness benefits to individuals who are able to exploit it (Albon & Langvatn, 1992; Middleton et al., 2018). As such, it underlies the evolution of cognitive abilities relating to navigation, perception, memory, and learning which ultimately determine where, when, how, and *if* an organism moves, and how plastic their movement behavior is (Fagan et al., 2013; Mery, 2013; McPeek & Holt, 1992; Morand-Ferron et al., 2016; Mueller & Fagan, 2008; Owen-Smith et al., 2010). In-turn, these abilities direct movement by allowing animals to respond to the contemporary predictability of their environment, which represents a crucial form of environmental information. Under this theoretical framework, environmental predictability both *underlies* and *directs* animal movement and space use. Increasing appreciation for the dual role of environmental predictability in determining species' cognitive abilities and serving as a source of environmental information has produced a fast-growing body of literature on the topic (Jonzén et al., 2011; Riotte-Lambert & Matthiopoulos, 2020; Teitelbaum & Mueller, 2019). Improvements in biologging and remote sensing technologies have furthered this research by improving our ability to determine how individuals respond to dynamic resource landscapes (Bautista et al., 2023; Crook et al., 2020; Neumann et al., 2015).

Although research has examined the relationship between predictability and movement behaviors at the species level, the mediating influence of environmental context is rarely considered despite the gradient of climatic and ecological conditions faced by populations of wide-ranging, habitat generalists. Populations of a given species inhabiting disparate landscapes are confronted with different suites of conditions that impose unique constraints on moving individuals (Strickland et al., 2005). As such, movement decisions – and the weight of factors incorporated into those decisions – may vary greatly from one population to another. Indeed, in many ungulate species we observe variation between populations in movement and space use tactics (Bolger et al., 2008), but the extent to which differences in environmental predictability – and its use as a form of environmental information – drives this intraspecific variation is seldom examined (but see research on roe deer, Morellet et al., 2013; Peters et al., 2019). Examining intraspecific variation in movement behavior and plasticity is important, as differences at the population level can impact large-scale community and ecosystem processes (Shaw, 2020).

Ungulates frequently face resource limitations that impact their survival (Kie, 1999) and therefore environmental conditions play a large role in their movement decisions (Sæther, 1997; Senft et al., 1987). At large scales, ungulates' movement tactics allow them to maximize access to high quality forage by timing relocations in accordance with vegetation dynamics and choosing areas with reliably available resources (Aikens et al., 2020; Bischof et al., 2012; Hebblewhite et al., 2008; Merkle et al., 2016). These strategies – observed at the species, population, and individual level – necessitate cognitive abilities and movement tactics that are, in theory, reliant on environmental predictability of resources; however, research regarding ungulate movement has often included the concept of environmental predictability as a factor posited to be encapsulated by the qualitative conditions of the study system (e.g., Martin et al., 2015; Joly et al., 2021) rather than as a quantitative metric that is empirically tested. In order to make more conclusive statements about the influence of environmental predictability on animal movement, integrating better quantitative methods into a theoretical framework is necessary.

Where predictability has been defined and considered in analyses, a large degree of variation exists. Most studies calculate predictability by quantifying some form of spatial or temporal variability or deviation of an environmental variable (most commonly forage, quantified with Normalized Difference Vegetation Index) (e.g., Bastille-Rousseau et al., 2017; Mueller et al., 2011). Several studies cite Colwell's (1974) pioneering work regarding order and disorder of environmental variables (Abrahms et al., 2021; Peters et al., 2019; Tonkin et al., 2017) and some research efforts (Couriot et al., 2018; Morrison et al., 2021) employ his decomposition of predictability into two separate metrics: constancy, *the inverse of the variability of resource conditions a) across space and b) throughout time*, and contingency, *the regularity of seasonal cycling*. These metrics capture unique components of an organism's resource landscape by identifying inter- and intra-annual predictability, respectively, and they represent predictability at different spatial and temporal scales.

Both scale and habitat quality are important to consider when studying the effect of environmental predictability on animal movement (Wiens, 1989). Movements occur at a wide range of spatial and temporal scales, (Benhamou, 2014; Fryxell et al., 2008; Owen-Smith et al., 2010) and predictability must be considered and calculated at an appropriate spatial scale for the type of animal movement considered. Research to date has mainly focused on the relationships between predictability and large-scale movement behaviors, by examining predictability across a populations' range area and relating that to behaviors such as migration (e.g., Mueller et al., 2011). Much less is known about environmental predictability in regard to animal movement at finer scales, where foraging decisions are predicated on food item value and costs associated with movement and digestion (Stephens & Krebs, 1986).

Additionally, the response of a species to the predictability of its environment may not be consistent throughout the year, as individuals' ecological requirements fluctuate seasonally (e.g., protein vs fat gain) (Johnson et al., 2021; Lesage et al., 2001; Monteith et al., 2011). Seasonal conditions can alter associated costs and benefits of movement (Gilbert et al., 2017; Robinson & Merrill, 2012; Sand et al., 2006), which may change animals' proclivity to use environmental predictability as a source of information when making movement decisions (Jonzén et al., 2011) or shift which type of predictability (spatial or temporal) provides the most relevant information. Finally, the benefit that ungulates derive from forage is a function of quality, quantity, and rumination dynamics (Fryxell, 1991; Hebblewhite and Merril, 2009; Van Soest, 2018). The tradeoffs between these factors are well documented to impact ungulate movement (Hebblewhite et al., 2008; Stratmann et al., 2023) and result in selective feeding behaviors (Esmaeili et al., 2021). Because ungulates select for forage quality forage at multiple scales (e.g., plant, patch, landscape) (Hebblewhite et al., 2008; Senft et al., 1987) and small changes in forage quality can increase nutrient intake (White, 1983), habitat quality also influences foraging dynamics and as a result affects movement and space use.

In this study I examine how environmental predictability acts as a source of environmental information driving movements of two populations of mule deer (*Odocoileus hemionus*) inhabiting disparate environments in Utah, USA. Specifically, I assess how spatial and temporal predictability of an individual's seasonal home ranges affect daily displacement under contrasting conditions of seasonality, forage quality, and home range area (Figure 1). Daily movement is indicative of deer time budget and energy balance which can impact overwinter survival (Bender et al., 2007) and litter size (Tollefson et al., 2010), which directly impact population parameters of mule deer. Movement also may make individual animals more susceptible to predation (Lima & Bednekoff, 1999). Finally, daily movement is an indicator of space required by an individual to meet its daily nutritional needs (Geist, 1981), which dictates the carrying capacity of the environment in question (Pastor et al., 1997).

Mule deer are well suited for this analysis because they have adapted to extreme environmental gradients, like those present in our study region of Utah, and there is a breadth of knowledge about their biology, ecology, and physiology (Heffelfinger, 2006). In addition, the small rumen to body size ratio of mule deer requires them to be more selective than other ungulates in their forage intake (Cox et al., 2009). This selectivity may result in strong observable responses to the predictability of the landscape. I hypothesize that vegetative productivity, as a proxy for forage quality, will mediate the relationship between movement decisions and environmental predictability. I also expect the population experiencing the most intense seasonal differences (North Slope of Utah), will respond more strongly to

environmental predictability within their home ranges relative to mule deer inhabiting the far less seasonal region in southern Utah (Pine Valley).

Mule deer are widely distributed and abundant across the American West, and understanding how environmental predictability relates to daily movement and space-use patterns is important for management of this ecologically, economically, and recreationally important species (Heffelfinger & Messmer, 2003), especially in increasingly modified and fragmented landscapes (Sih et al., 2011). As environmental predictability and habitat quality wane under the increasing intensity of climate change and human development, integrating measures of environmental predictability into wildlife studies will become increasing critical to make correct inference.

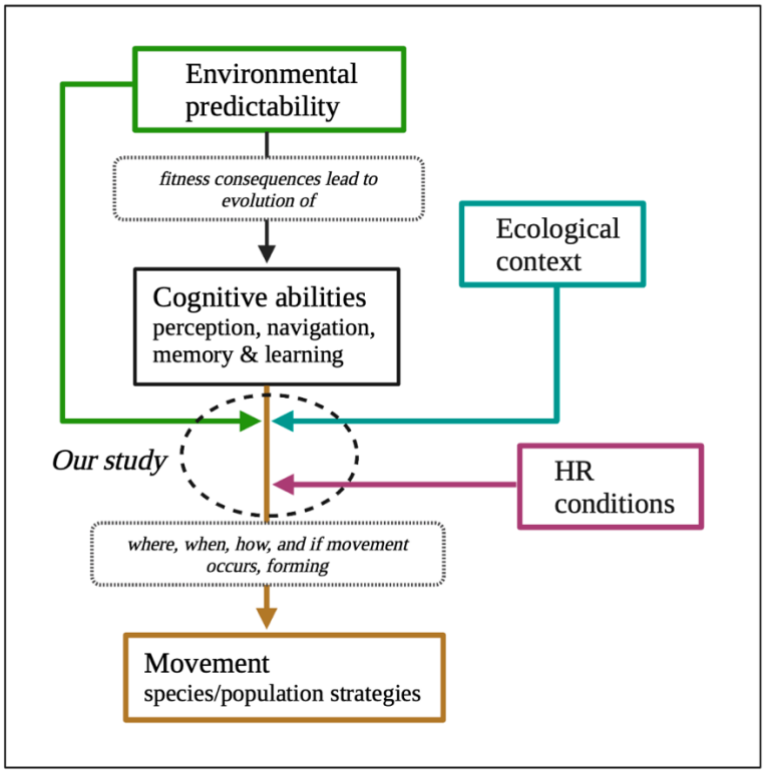


Figure 1 Visual depiction of how this study (denoted by the dashed circle) fits into the larger environmental predictability paradigm. Components that are empirically tested are indicated in colored boxes.

Methods

Mule deer GPS data

Mule deer were captured using the helicopter net-gun technique (Jacques et al., 2009) and fitted with GPS collars (model type G2110E2H, G5-2DH, or W300; Advanced Telemetry Systems, Isanti, MN, USA) by the Utah Department of Wildlife Resources (UDWR) spanning the years 2015-2023 (see Van de Kerk et al., 2020 for details). Professional capture and ground crews handled animals following the most current version of the guidelines for the use of wile mammal species laid out by the American

Society of Mammologists (Sikes et al., 2011). Mule deer in Utah are classified into defined wildlife management units by the UDWR. Here I utilized data from two management units, one in the northeast corner of the state, the North Slope (306,470 ha), and one in the southwest, Pine Valley (350,980 ha). As movement was not constrained by state boundaries, home ranges extend into Wyoming for deer in North Slope, and into Nevada for deer in Pine Valley (Figure 2).

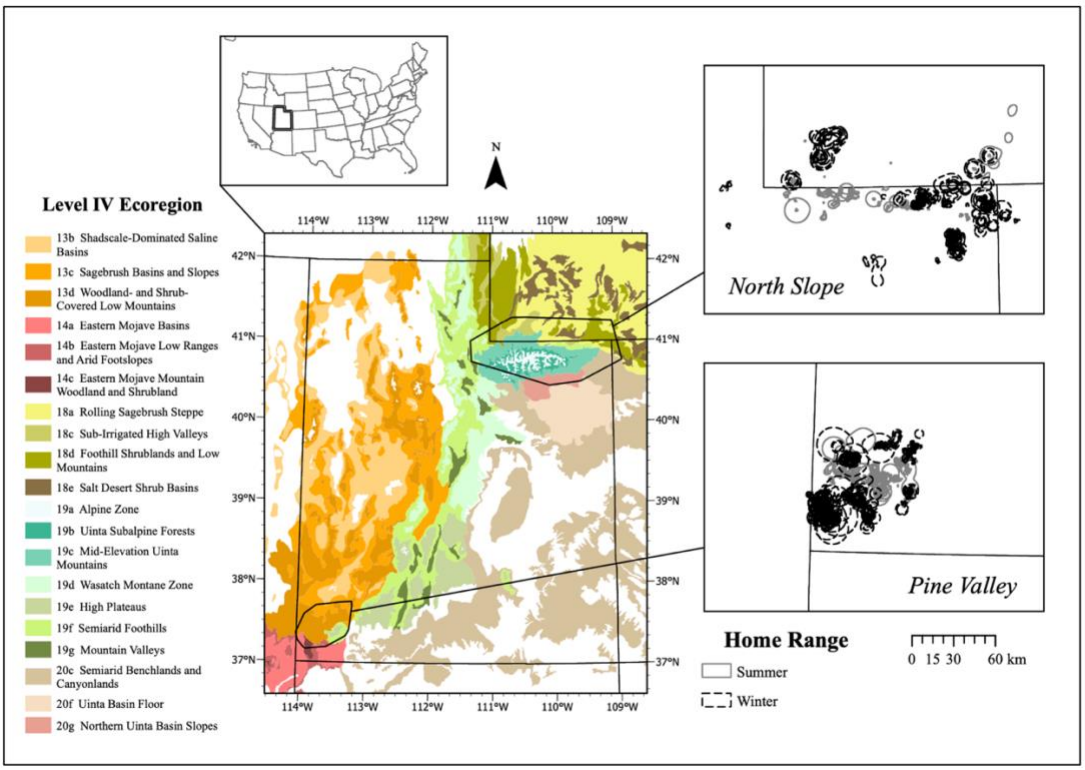


Figure 2 Map of study areas in Utah, USA. Ecoregions (Level IV) were only displayed if intersecting with or relevant to home range locations. Minimum convex polygons used to denote study areas were created from home range centroids. Summer and winter home range areas represent 95% Kernel Utilization Distributions (Kernel UD).

Seasonal home range characteristics

Utah is a land of contrast, and the state is characterized by extreme variations in elevation (Banner, 1992), which results in distinct spatial patterns of interrelated environmental factors such as precipitation, temperature, and evapotranspiration. Together these factors determine the amount and type of vegetation that occurs in any given environment across the state. Like most ungulate species in the Intermontane West (Fryxell & Sinclair, 1988; Garrott et al., 1987; Monteith et al., 2011), mule deer in these populations spend the summer months in high elevation areas and return to lower elevation areas in the winter. Characteristics of summer and winter home range areas for both populations are summarized in Table 1 (Omernik, 1987, Omernik, 1995, Ramsey & West, 2009; U.S. Environmental Protection Agency, 2000; UDWR, 2020, a&b).

In temperate environments, forage quality and availability are generally lower in the winter, and as such, movements should reflect the need to access forage while keeping energetic costs low; however, energetics and outcomes of movement in the winter are markedly different for individuals in these the two populations. The North Slope has deep winter snowpack that can function to hinder or prevent movement and restrict access to forage (Parker et al., 1984; Parker et al., 2009; Robinson & Merrill, 2012), and cold seasonal temperatures in that region require increased energy to maintain homeostasis. For deer inhabiting areas like the North Slope, winter forage is considered a mere subsidy, and individuals must rely largely on fat reserves gained during the summer to sustain them through the harsh winter (Bishop et al., 2009). In Pine Valley, winter snow is ephemeral, and temperatures are mild enough to provide forage, although of a lower quality, for most of the winter season.

In the summer, forage quality and availability are higher. For ungulates like mule deer, summer is a crucial and energetically demanding time, as individuals may have to balance movement constraints imposed by their young (Bowyer et al., 1998; Loudon et al., 1983) and the need to accumulate body fat before winters onset (Parker et al., 2009; Cook et al., 2004). Again, these assumptions are nuanced by the ecoregion inhabited by the population in question, as the temporal dynamics of summer forage quality are different between these two study regions. In North Slope, higher altitude summer home ranges have prolonged snowmelt and cooler temperatures, which has been demonstrated to produce higher quality forage and lengthen the growing season in such ecosystems (Albon & Langvatn, 1992; Parker et al., 2009; Goodson et al., 1991). During this time individuals must replenish body fat lost during the previous winter and ensure that they have a favorable ratio of energy intake to expenditure so as to accumulate enough body fat to survive the coming winter (Moeslund et al., 2013). The semi-arid environment in Pine Valley limits net primary productivity, and forage quality declines earlier in the season in comparison to the North Slope. In arid environments, water is often a key limiting resource for organisms and for the forage upon which animals depend (Nandintsetseg et al., 2019; Cox et al., 2009) and mule deer movements are often constrained by proximity to water (Shields et al., 2012).

Table 1 Seasonal home range information.

Range	*Ecoregion (Level IV) // Life Zone(s)*	*Climate & Hydrology*	*Natural Vegetation*	*Ownership // Land Use*
North Slope Summer  Krahulec, K	Mix of mid-elevation Uinta mountains (2438 – 3048 m) // Mountain and High Mountain AND Subalpine Forests (3048 – 3353 m) // Subalpine.	Mean annual snowfall is between 20-30+ inches and exceeds 70 inches in mid-elevation and 150 inches in highest regions. Good quality perennial streams are found in deep canyons.	Mountain and high-mountain regions dominated by Douglas-fir forest with lodgepole and ponderosa pine, aspen parkland, and a sagebrush and forb understory. In lower riparian areas willow and cottonwood are present. In subalpine areas western spruce-fir forest exists with lodgepole pine and aspens interspersed. Subalpine understory consists of mainly sedge.	Forest Service (87%) and Private (8%) // Mostly wildlife habitat with some logging, seasonal rangeland, and water supply.
North Slope Winter  Cox, S	Mainly semiarid benchlands and canyonlands (1524 – 2286 m), semiarid bear hills (1935 – 23467 m), and wet valleys (1829 – 2012 m), with some semiarid foothills (1524 – 2438 m) // all Upland.	Between 10-16 inches of rain annually, reaching up to 25 inches at higher elevation semiarid foothills, canyonlands, and benchlands. Some streams occur in semiarid foothill areas, originating from higher elevation regions.	Wet valleys contain sagebrush steppe, sedges, alkali sacaton and bluegrass. Juniper woodlands and sagebrush occur in semiarid bear hills. Higher elevation foothills are dominated by juniper-pinyon woodland, sage-parkland, and mountain brush.	Forest Service (42%), Bureau of Land Management (24%), Utah State Institutional Land Trusts (11%), and Private (21%) // Rangeland, pasture, and some irrigated agriculture in lower elevation areas. Some areas contain oil/natural gas fields. Woodland grazing in semiarid bear hills.

Pine Valley Summer  Hanser, S	Mainly woodland and shrub covered low mountains (1524 – 2743 m) // Semidesert.
	
	Some semiarid foothills (1524 – 2438 m) // Upland.
	
	Some high plateau (2438 – 3353 m) // Mountain.
		High plateau areas receive between 16-40+ inches of rain annually and have a deep winter snowpack which provides water to lower elevation mountains and foothills during the late spring and summer where rainfall averages 10-22 inches annually. Streams in lower elevation areas are ephemeral.	Juniper-pinyon woodland and sagebrush co-dominate at low elevations. Mountain mahogany-oak scrub and ponderosa pine occur in semiarid foothills. Spruce, fir, and pine forests dominate high plateau areas with aspen stands occurring on south facing slopes.	Forest Service (67%), Bureau of Land Management (11%), Wilderness areas (15%) // Rangeland, woodland, and logging at low elevations. Water supply and heavy seasonal grazing on high plateaus.

Pine Valley Winter  NPS	A mix of creosote bush-dominated basins (671 – 1219 m), woodland and shrub covered mountains (low and high, 1219 – 2743 m), and sagebrush basins and slopes (1341 – 2255 m) // all Semidesert	Between 6-12 inches of rain annually in low elevation basins and increasing to 10-22 in mountainous areas. Snow is ephemeral.	Creosote bush dominates in lowest elevation arid basins along with Joshua-tree and several grasses. Juniper-pinyon woodland and sagebrush occur in lower elevation mountains and basins. Higher elevation mountainous areas are covered in mountain brush and juniper-pinyon woodland.	Forest Service (38%), Bureau of Land Management (44%), Private (13%) // Rangeland and woodland at higher elevations with logging and irrigated farming at lower elevations.

Season determination

Our goal was to examine movement occurring within a seasonal home range, so I delineated seasons based on timing of movements between summer and winter range areas, excluding days during which these movements occurred (referred to as the "shoulder"). Shoulder dates were determined for each study region by identifying the Julian days at which the rate of change of the average net-squared-displacement (NSD) was the greatest. NSD was calculated using the *amt* package (version 0.1.6; Signer et al., 2011) in R software (R Core Team, 2023) and represented the straight-line displacement from an individual's location on January 1. After delineating season start and end dates, I excluded individuals if they did not have locations for at least 2/3 of the days within the season. Number of locations was not significantly correlated with home range area or daily distance (Supplementary Table 1). Seasons were delineated separately for each capture unit (Supplementary Table 2).

Animal home range and daily movement

GPS collars acquired fixes at intervals between 2-24 hours; however, the majority (>80% of individuals) collected locations at either 2 or 12-hour frequencies. Prior to analysis, all trajectories were re-sampled to a frequency of 12 hours to minimize frequency impacts on calculated individual home range areas. The average distance moved per day within the summer and winter ranges was measured by summing the distance (m) between each relocation, calculated with *move* (version 4.1.10; Kranstauber et al., 2021), and dividing the total by the number of days of data that each individual had during that season. To identify the spatial limits for quantification of environmental predictability and quality, I estimated each individual's year-specific summer and winter home ranges (ha) using a 95% kernel density estimate in *adehabitatHR* (version 0.4.20; Calenge, 2006), employing an *ad hoc* method for smoothing (supported by Bowman, 1985; Schuler et al., 2014; Worton, 1989). After excluding individuals based on the above season-specific criteria, our final set of home ranges included 225 unique individuals (*North Slope*, n = 66; *Pine Valley*, n = 159) for a total of 880 seasonal home ranges (*North Slope*

Summer, n = 119; *North Slope Winter*, n = 151; *Pine Valley Summer*, n = 248; *Pine Valley Winter*, n = 362). I used these 95% home ranges to extract remotely sensed vegetation metrics used to calculate habitat quality and predictability.

Habitat indices

To quantify metrics for predictability and habitat quality, I used Normalized Difference Vegetation Index (NDVI) derived from MODIS satellite imagery (MOD13Q1.061 product) with a 250-meter spatial resolution and a 16-day temporal resolution. NDVI imagery was collected via Google Earth Engine for years 2011-2022 (Gorelick et al., 2017) and rescaled from -1.0 to 1.0. NDVI is commonly used as a proxy for forage availability and quality and has been demonstrated to be accurate at predicting resource availability and productivity for herbivores such as ungulates (Hamel et al., 2009; Pettorelli et al., 2005; Ryan et al., 2012). In addition, NDVI has high temporal resolution and has consistent coverage and utility across diverse landscapes. The mean NDVI was calculated across all composites with dates within a given season using all pixels within the individual's home range.

Following Colwell's (1974) definition of predictability and employing the methodologies of Morrison et al (2021), constancy (C) was calculated using Shannon's entropy (H) (1948). For our constancy calculations, 100 intervals (n = 100) were employed in the Shannon's Entropy calculation to find the proportion of pixels (P_i) falling within each interval between the minimum and maximum value.

$$C = 1 - H/log(n)$$

$$H = -\sum P_i \, x \, log(P_i)$$

Temporal constancy, the variance in NDVI value of an individual pixel through time, was calculated on a pixel basis and then averaged across the entire home range (Figure 3, top). Spatial constancy, the instantaneous variance of NDVI across an individual's seasonal home range, was calculated across each 16-day NDVI composite and then averaged through the entire season (Figure 3, bottom). Both spatial and temporal constancy ranged from 0 to 1, representing low and high predictability, respectively. Finally, I calculated the mean NDVI across the home range for the entire season, including all composites, which represented the overall forage quality of the home range.

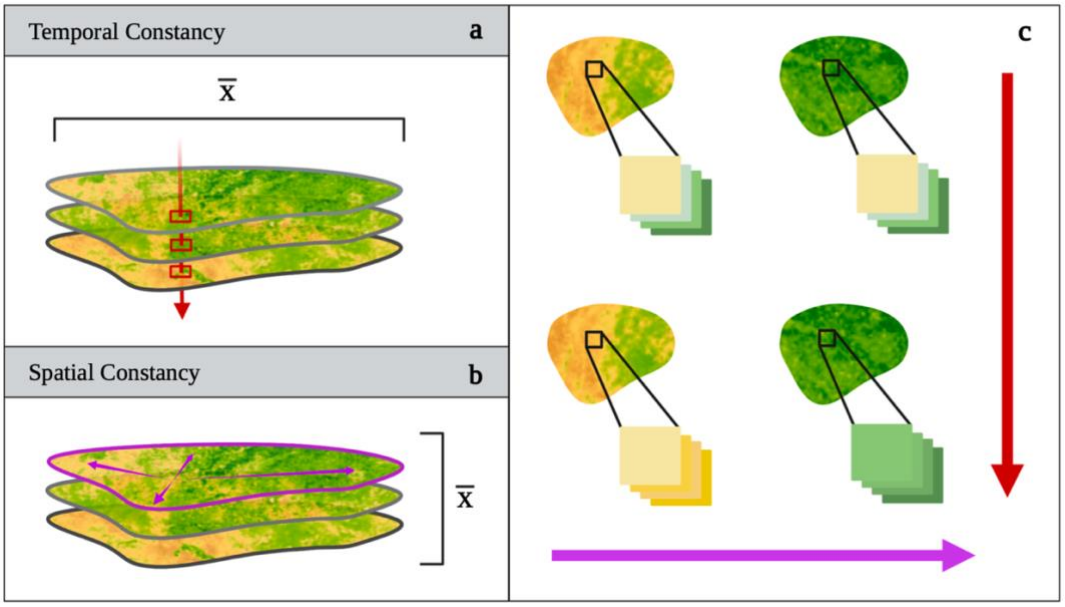


Figure 3 Visual representation of temporal (a) and spatial (b) constancy calculation and visualization comparison of constancy of hypothetical home ranges. X-bar represents final average taken over the entire home range (a) or the entire length of the season (b) to produce the final temporal and spatial constancy values for each individuals' seasonal home range. In c, spatial constancy increases moving from left to right and temporal constancy increases moving from top to bottom.

Regression of predictability and home range area

I observed high correlation between home range area and our two metrics of predictability (Supplementary Figure 2 a & b). This relationship was not unexpected, as variability inherently increases as the area over which these metrics were calculated increases. As one of the goals of this study was to determine if environmental predictability could explain variation in daily movement unrelated to range area, we regressed the variables of home range area and predictability, both spatial and temporal, to calculate residual values for each seasonal home range. In the field of landscape ecology, indexes are commonly used to compare different landscapes, and I employ these residuals values here as a form of habitat index to represent the relative predictability of a home range given its size, with positive values indicating a more predictable area, and negative values representing a less predictable area (Turner, 1989). I employed a third-degree polynomial for these regressions and ran separate regressions for each combination of season and population.

It is important to note that while these metrics of predictability were calculated using NDVI values, they do not represent a metric of resource quality. A high value of predictability does not correspond to high NDVI, rather, it indicates that resources are consistent, either in space or time – these resources could be predictably "bad" or "good".

Modeling approach

Linear mixed-effects models (LMM) were used to determine how daily displacement varied between populations and across seasons, and test what drives this variation. Both home range area (ha) and our response variable (daily distance, m) were log transformed prior to analysis – and prior to regression with our predictability metrics in the case of home range area – to normalize their distribution. Data was then standardized (scaled and centered, as suggested by Schielzeth, 2010) in order to be able to compare effect sizes between models and interpret main effects in the presence of interaction terms (Engqvist, 2005). LMM (lme4, version 1.1-32; Bates et al., 2015) allowed us to incorporate animal ID and year as random effects that could account for consistent individual differences in movement (Montgomery et al., 2018) and effects of yearly stochastic weather (Ogutu et al., 2014). Because home range area and daily distance are mechanistically correlated (Börger et al., 2008; Moorcroft & Lewis, 2013; Viana et al., 2018), I included home range area as a predictor of daily distance. I modeled this relationship using a spline (df = 3) to account for its clear non-linear nature (Supplementary Figure 1). All other main effects and interaction terms were modeled with linear relationships.

I ran four linear mixed models for each combination of season (spring and winter) and population (North Slope and Pine Valley). Our final model structure included the main effects of spatial constancy, temporal constancy, forage quality, home range area, and interactions terms for spatial & temporal constancy × area, spatial & temporal constancy × forage quality, and spatial constancy × temporal constancy, for a total of 9 fixed effects and two random effects (year and animal ID). The same fixed and random effects' structure was used for all models. Parameter estimates were obtained using Restricted Maximum Likelihood (REML) to avoid bias in variance components assigned to fixed and random effects (Nakagawa & Schielzeth, 2013; Pinheiro & Bates, 2006).

Results

Population differences

Forage quality was higher in summer range areas than during the winter for both populations, but values were more variable during summer (Table 2, Figure 4). Home range areas were smaller in the summer than the winter for both populations. (Table 2, Figure 4). Average daily distance was similar between seasons in the North Slope, but individuals in Pine Valley had greater daily movements during the winter than during the summer on average (Table 2, Figure 4).

Table 2 Summary mean (x), standard deviation (σ), and confidence interval (CI) of forage availability (mean NDVI), home range area (ha), and daily distance (m) for each combination of season and capture unit.

			Statistic		
Range			***NDVI***	***HR Area***	***Daily Distance***
Summer					
	North Slope	x	0.589	1583.54	1139.52
		σ	0.085	5127.89	393.69
		CI	0.573 - 0.604	652.66 - 2514.41	1068.05 - 1210.99
	Pine Valley	x	0.543	1787.41	831.51
		σ	0.069	5470.86	499.85
		CI	0.534 - 0.552	1103.17 - 2471.66	768.99 - 894.03
Winter					
	North Slope	x	0.290	5989.80	1046.22
		σ	0.047	9809.27	259.51
		CI	0.282 - 0.297	4412.50 - 7567.10	1004.49 - 1087.95
	Pine Valley	x	0.380	3559.36	1315.00
		σ	0.036	9780.10	495.09
		CI	0.377 - 0.384	2548.49 - 4570.23	1263.83 - 1366.18

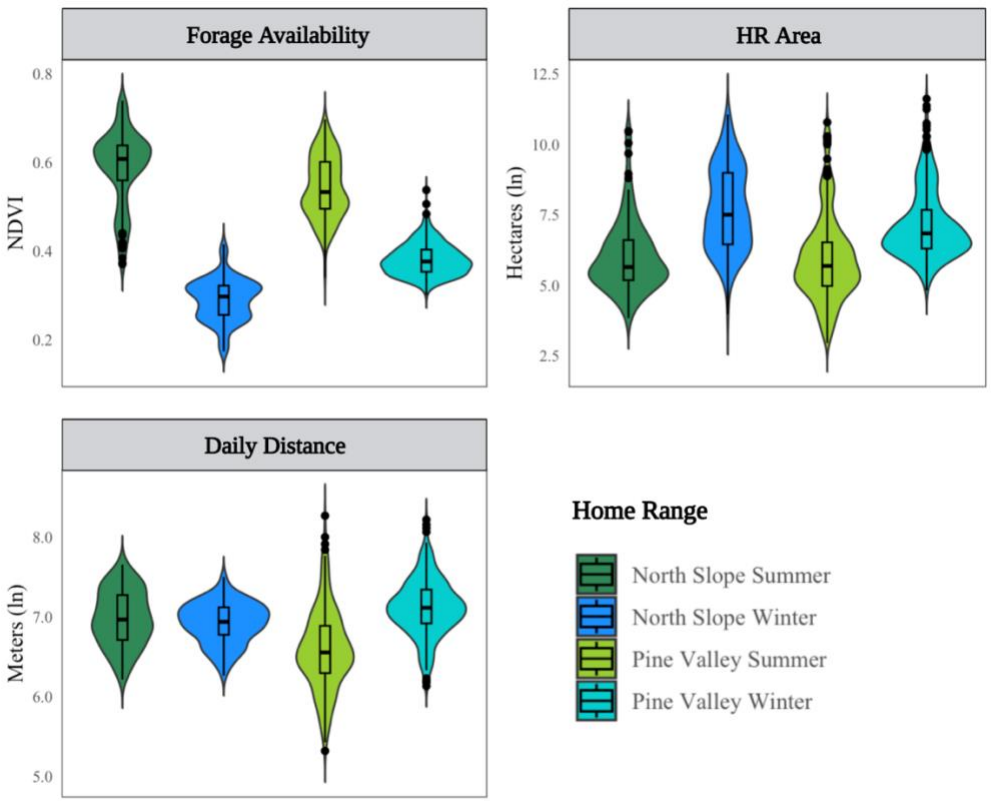


Figure 4 Summary violin plots of home range forage availability and area, and daily distance values. Values for area and distance are natural log transformed.

Model results

Increased forage quality within an individual's seasonal home range resulted in greater daily movement in the winter (*North Slope*, x = 0.225, p = <.001*; *Pine Valley*, x = 0.085, p = 0.144) and shorter movements during the summer (*North Slope*, x = -0.012, p = 0.641; *Pine Valley*, x = -0.232, p = <.001*). Daily movement distances of mule deer increased with greater estimated spatial predictability – representative of the average "instantaneous" homogeneity of NDVI values across an area – at the home range scale (*North Slope winter*, x = 0.051, p = 0.172; *Pine Valley summer*, x = 0.134, p = <.001*; *Pine Valley winter*, x = 0.041, p = 0.145). The exception to this relationship was in the North Slope during the summer, where greater spatial predictability was associated with significantly shorter daily movements (*North Slope summer*, x = -0.065, p = 0.021*). Daily movement of deer decreased with greater temporal predictability – representative of the average homogeneity of a single NDVI pixel over the entire season – (*North Slope summer*, x = -0.106, p = 0.006* ; *Pine Valley summer*, x = -0.014, p = 0.665; *Pine Valley winter*, x = -0.063, p = 0.045*); however, in the North Slope in the winter, animals moved greater distances in more temporally predictable landscapes (*North Slope winter*, x = 0.064, p = 0.279). Random effects of year and animal are summarized in the supplementary material (Figure 4 & 5).

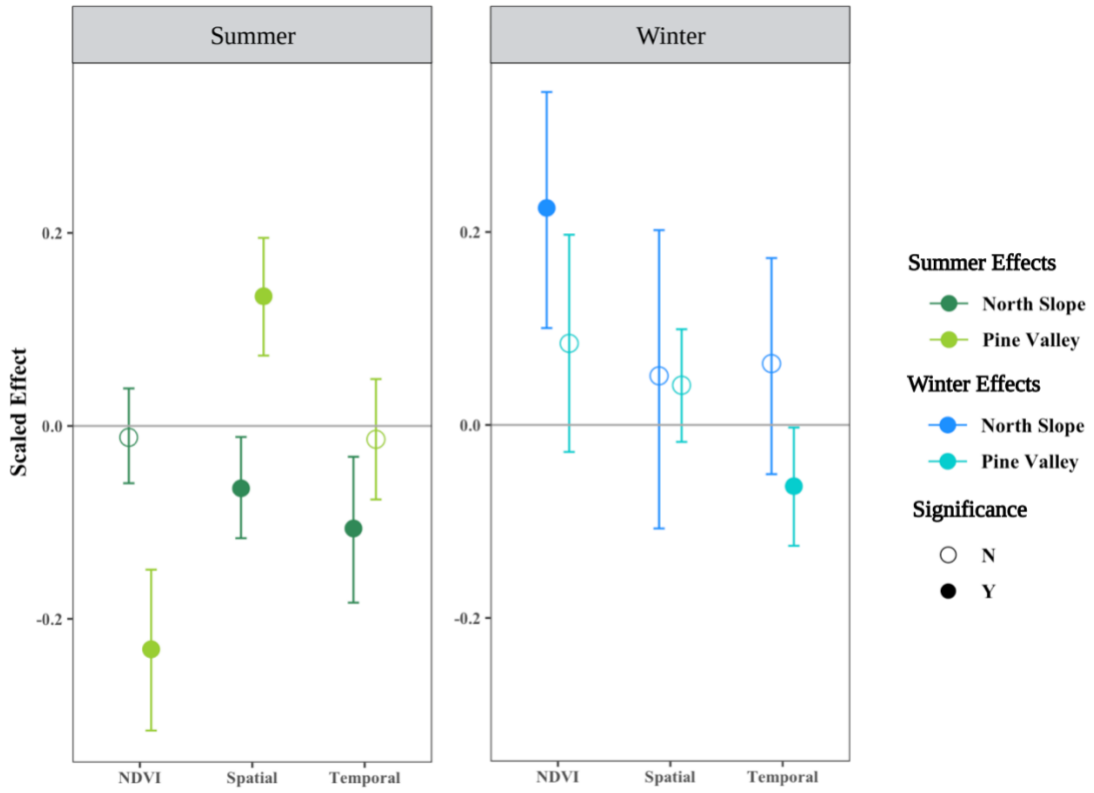


Figure 5 Effect plot for main effects in mixed effects models. Values are scaled.

In the North Slope, I found significant interactive effects between summer home range area and both metrics of predictability. As summer home range area increased, the negative significant effects of both spatial (x = -0.065, p = 0.021*) and temporal (x = -0.106, p = 0.006*) predictability became greater (*spatial:area*, x = -0.048, p = <.001*; *temporal:area*, x = -0.093, p = 0.004*), and daily movements of deer decreased (Figure 6). Deer in Pine Valley exhibited similar relationships between summer home range area and temporal predictability (x = -0.041, p = 0.135) and winter home range area and spatial predictability (x = 0.027, p = 0.070), however these relationships were not statistically significant. See supplementary material for plots depicting non-significant interactions between home range area and predictability (Supplementary Figures 3a & b).

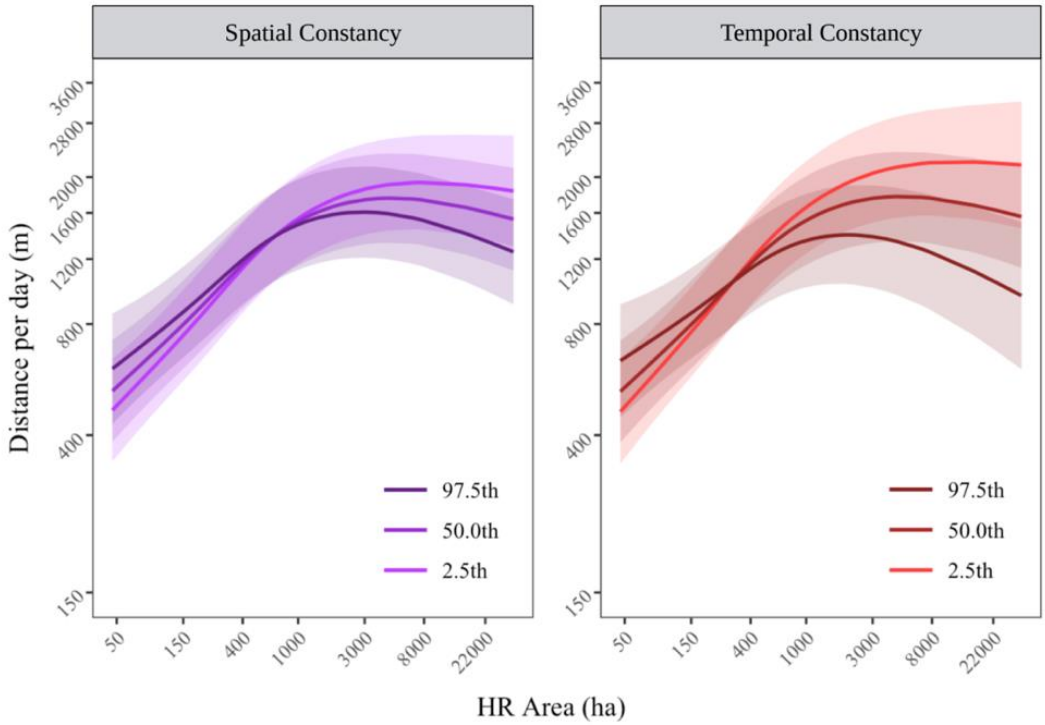


Figure 6 Interaction plot between summer home range spatial (left) and temporal (right) constancy and area for the North Slope. Lines represent the marginal effects of the 97th, 50th, and 2.5th percentile values of spatial and temporal constancy, corresponding to high, normal, and low predictability respectively. Random effects were incorporated into predictions and are reflected in the confidence intervals, shown by the shaded region corresponding to each marginal effect level. Calculated confidence intervals were based on standard errors, assuming a normal distribution with ggeffects (version 1.2.3).

During the summer, the effect of spatial predictability on daily movement was modulated by forage. In the North Slope, high spatial predictability tended to result in smaller daily movements; however, as forage quality increased, deer inhabiting spatially predictable home ranges moved significantly more than deer with unpredictable home ranges (*spatial:NDVI*, $x = 0.046$, $p = 0.022$*). In Pine Valley, spatial predictability resulted in larger daily movement; however, as forage quality increased, deer inhabiting spatially predictable home ranges moved less per day than deer with unpredictable home ranges (*spatial:NDVI*, $x = -0.091$, $p = 0.016$*). See supplementary material for plots depicting non-significant interactions between forage availability and constancy (Supplementary Figure 3c).

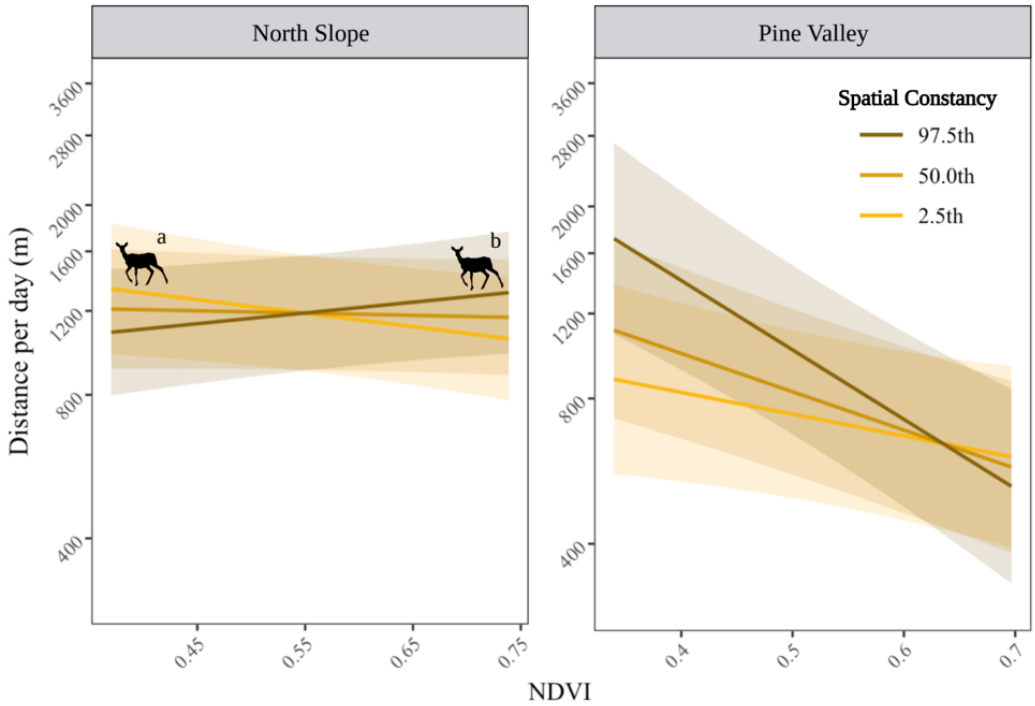


Figure 7 Interaction plot between North Slope (left) and Pine Valley (right) spatial constancy and NDVI in the summer. Lines represent the marginal effects of the 97th, 50th, and 2.5th percentile values of spatial and temporal constancy, corresponding to high, normal, and low predictability respectively. Random effects were incorporated into predictions and are reflected in the confidence intervals, shown by the shaded region corresponding to each marginal effect level. Calculated confidence intervals were based on standard errors, assuming a normal distribution with ggeffects (version 1.2.3).

In Pine Valley during the summer, increased temporal predictability functioned to reduce the positive effect of spatial predictability on daily distance (*spatial:temporal*, x = -0.043, p = 0.028*). I did not observe significant interactions between these predictability metrics in any other models. See supplementary material for plots depicting non-significant interactions between spatial and temporal constancy (Supplementary Figure 3e).

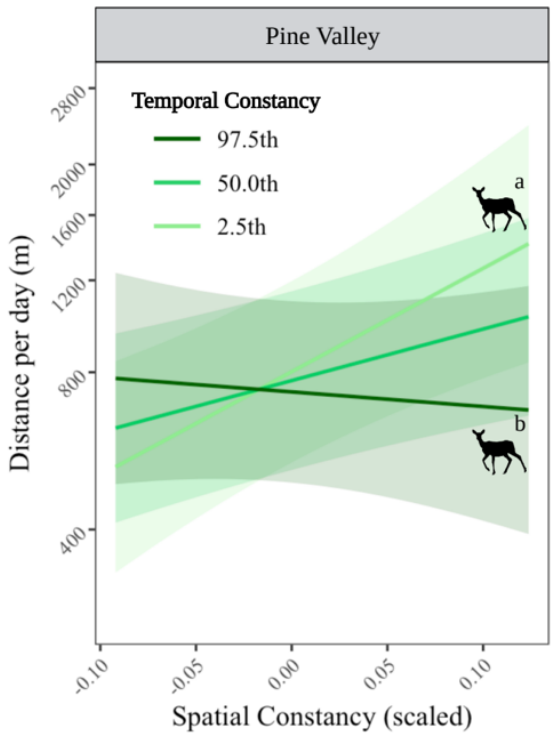


Figure 8 Interaction plot between summer spatial constancy and temporal constancy for Pine Valley. Lines represent the marginal effects of the 97th, 50th, and 2.5th percentile values of spatial and temporal constancy, corresponding to high, normal, and low predictability respectively. Random effects were incorporated into predictions and are reflected in the confidence intervals, shown by the shaded region corresponding to each marginal effect level. Calculated confidence intervals were based on standard errors, assuming a normal distribution with ggeffects (version 1.2.3).

Table 3 Summary of coefficient estimates (β) and confidence intervals (CI) for linear mixed models. Effects are scaled for all models.

			Main Effects				***Random Effects***	
Model			***NDVI***	***Spatial***	***Temporal***		***Animal***	***Year***
Summer	*North Slope*	β	-0.0119	**-0.0647**	**-0.106**	σ^2	0.00715	0.000601
		CI	-0.0593 – 0.0390	**-0.116 – -0.0115**	**-0.183 – -0.0320**	σ	0.0846	0.0245
	Pine Valley	β	**-0.23154**	**0.134**	-0.0139	σ^2	0.0371	0.00570
		CI	**-0.316 – -0.149**	**0.0729 – 0.195**	-0.0764 – 0.0486	σ	0.193	0.0755
Winter	*North Slope*	β	**0.225**	0.0510	0.063637	σ^2	0.0241	0.00460
		CI	**0.100 –0.345**	-0.107 – 0.202	-0.0510 – 0.173	σ	0.155	0.0678
	Pine Valley	β	0.0846	0.0413	**-0.0634**	σ^2	0.0693	0.00399
		CI	0.0279 – 0.197	-0.0175 – 0.0992	**-0.125 – -0.00266**	σ	0.263	0.0631

			Interactions				
Model			***NDVI:Spat***	***NDVI:Temp***	***Area:Spat***	***Area:Temp***	***Spat:Temp***
Summer	*North Slope*	β	**0.046339**	0.033543	**-0.0478**	**-0.093095**	0.002653
		CI	0.00624 – 0.0832	-0.0104 – 0.0783	-0.0728 – -0.0224	-0.156 – -0.0342	-0.0410 – 0.0464
	Pine Valley	β	**-0.0911**	-0.0363	-0.0253	-0.0408	**-0.0435**
		CI	-0.165 – -0.0175	-0.0923 – 0.0201	-0.0582 – 0.00741	-0.0931 – 0.0117	-0.0814 – -0.00557
Winter	*North Slope*	β	-0.019694	0.051557	-0.035030	0.00507	-0.012669
		CI	-0.146 – 0.101	-0.0361 – 0.136	-0.0726 – 0.00153	-0.0332 – 0.0408	-0.0560 – 0.0303
	Pine Valley	β	0.082815	-0.006070	0.0271	0.0367	-0.006526
		CI	-0.0143 – 0.178	-0.107 – 0.0943	-0.00188 – 0.0558	-0.0173 – 0.0895	-0.0395 – 0.0263

Discussion

Empirical studies have related metrics of environmental predictability to animal movement behaviors at multiple scales (Bauer et al., 2020; Morrison et al., 2021; Mueller et al., 2011), but the relationship between the predictability of forage and daily movement within an individual's seasonal home range has not been investigated until now. My study demonstrates that environmental predictability impacts habitat use of mule deer at fine scales. I found that both spatial and temporal constancy were significant predictors of daily movement and that spatial constancy had significant interactions with home range area and forage availability. Additionally, my results indicate that spatial and temporal constancy interact to

inform movement in certain limiting environments. Importantly, I observed that population- and season-specific ecological constraints seemed to dictate these relationships.

Although I expected that individuals in the North Slope would show a greater response to environmental predictability than those in Pine Valley, I saw strong and significant responses to spatial and temporal constancy in both populations. Additionally, I expected that forage abundance would be an important determinant of daily movement by mule deer and modulate animals' response to environmental predictability; however, it was not a significant factor in all seasonal environments. That I observed such stark differences (in both direction and magnitude) in the response to environmental predictability between the two populations indicates that these populations have established wholly unique foraging tactics to deal with their ecological conditions.

When discussing the potential mechanisms underlying these results, one must consider the limiting qualities of these seasonal environments. The high temperatures and arid environment of Pine Valley make this environment "summer limited", and the precipitation regime renders the nutritional benefit of forage in this system lower relative to the North Slope, where prolonged snowmelt and cooler temperatures support continued plant growth and quality (Hurley et al., 2014; McKinney, 2003; Marshal et al., 2005). The North Slope is "winter limited" as harsh conditions and heavy snowpack physically hinder movement and increase associated energetic costs (Hudson et al., 2002), and so the nutritional benefits of forage must outweigh the cost of movement to acquire it. However, in Pine Valley, winter conditions are mild, and snow is ephemeral.

The observed relationships between spatial predictability and daily distance traveled within a seasonal home range are both reflective of these environmental limitations and indicative of the information captured in our predictability metrics. Spatial constancy quantifies the similarity of NDVI values across a given area and was employed in this study to understand spatial predictability of forage; however, the NDVI values used in these calculations also may capture functional aspects of the landscape such as aspect, slope, and cover, which determine landscape heterogeneity. As such, high values of spatial constancy may signify a more homogeneous home range.

Empirical studies on large herbivores have found that landscape heterogeneity impacts multiple aspects of movement and fitness outcomes (Fronhofer et al., 2013; Giralt-Rueda & Santamaría, 2023; Turner et al., 1997; Roese et al., 1991). In heterogeneous environments, elk had longer daily movements (Morales et al., 2005), and woodland caribou moved faster, which increased their encounter rate with forage (Avgar et al., 2013). Additionally, it has been suggested that in homogeneous areas, the costs of movement outweigh the limited foraging benefit from a new but similar

area (Switzer, 1993); a trade-off which may explain the significantly shorter daily movements I observed for some individuals inhabiting spatially predictable home ranges. While spatial constancy of resources in an individual's home range was a significant determinant of daily movement during the summer for both populations of mule deer investigated in this study, it resulted in *grater* movement in Pine Valley (our "summer-limited" population) and *less* movement in the North Slope (our "winter-limited" population).

These contrasting relationships demonstrate the use of environmental predictability as a source of environmental information incorporated into practical foraging strategies that enable animals in these populations to meet nutritional and life-history requirements. Increased movements in spatially predictable home ranges of deer in Pine Valley represent a strategy for meeting nutritional requirements in this arid environment. In this population, individuals may move greater distances through spatially "homogeneous" but poorer quality resource landscapes and select for nutritional quality or moisture content at the plant or bite level to reduce digestive processing capacity limitations from poor-quality forage or meet water requirements (Collins & Urness, 1983; Manser & Brotherton,1995; Owen-Smith, 1994; Van Soest, 2018; Baharav & Rosenzweig, 1985). The tradeoff between forage quality and size proposed by the forage maturation hypothesis (Fryxell, 1991) is well documented to impact ungulate movement, and research suggests that deer become more selective as available forage quality decreases (Hanley, 1997) which is reflected in multiple aspects of their foraging behavior (*time per bite*, Weckerly, 1994; *rate of travel*, Wickstrom et al., 1984; *time spent*, Wilmshurst et al., 1995; *distance*, Owen-Smith, 2013).

For deer inhabiting the non-limiting summer range of the North Slope, the benefits of movement in spatially predictable home range areas – access to forage which may be only minimally better than in their current location – may not outweigh the cost of expending energy – which depletes fat stores that individuals need for overwinter survival – resulting in less movement in spatially predictable summer home ranges within this population (Stephens & Krebs, 1986; Switzer, 1993). Travel costs are an important factor in ungulate foraging decisions (WallisDeVries, 1996; Murray, 1991), and energy associated with travel is mediated by terrain conditions (Dailey & Hobbs, 1989), and can increase exponentially in alpine habitats (Fancy & White, 1987). As such, the observed foraging strategy of deer in this environment consists of movement minimization within nutritionally homogeneous environments.

Our results also reveal that these foraging strategies are modulated by relative forage availability within an individual's home range. While spatial predictability was associated with shorter daily movement in North Slope during the summer, as forage availability increased within the home range, deer inhabiting spatially predictable home ranges traveled more per day than deer inhabiting home ranges with available

forage that was unpredictable in space (Figure 7). As such, deer in the North Slope inhabiting areas with available forage that was spatially predictable (Figure 7, individual b) moved similar distances per day to deer in areas with less forage that were unpredictable across space (Figure 7, individual a). As forage availability increases in this seasonal environment, energetic constraints on foraging may be relaxed, and individuals may forage more selectively in spatially predictable home range areas by searching for high-quality/rare species that confer the greatest benefit, increasing daily movement in the process (Murden & Risenhoover, 1993; Stephens & Krebs, 1986; Hehman & Fulbright, 1997). Simply put, as forage availability increases, movement to a new location may become "worth it".

In Pine Valley, spatial predictability of the home range resulted in greater daily movement within it, but as forage availability increased, the positive effect of spatial predictability on daily movement decreased. I observe that within home ranges at all levels of spatial predictability, deer moved relatively similar distances when forage quality was high (Figure 7). In this population, increased forage availability likely functions to release individuals from selective foraging requirements imposed by their limiting environment and renders spatial constancy "obsolete" as a source of environmental information driving movement. In summation, when considering the impact of forage availability in these environments, greater forage availability within a spatially predictable summer home range may incite more movement in the North Slope, by providing the opportunity for animals to select high-grade forage, but results in less daily movement in Pine Valley by releasing animals from nutritional constraints that necessitated movement-intensive foraging behavior.

Temporal constancy – invariance of NDVI throughout the season – was associated with significantly shorter daily movements in non-limiting seasonal environments; in home ranges with high temporal constancy of forage, deer in North Slope moved less during the summer while deer in Pine Valley moved less during the winter (Figure 5). High temporal constancy may be indicative of landscape features such as water sources that support continued plant growth and quality throughout the season (McLaughlin et al., 2017), and influence plant succulence (Noy-Meir, 1973). When studying ungulate species inhabiting environments similar to that of Pine Valley winter home ranges, Nandintsetseg et al (2016) found that water resources largely determined movement and constrained distances animals could move, and studies on mule deer have shown that animals change their distribution and movements relative to water sources, especially in desert-like conditions (Hervert & Krausman, 1986; Rautenstrauch & Krausman, 1989).

Finally, while temporal constancy alone was not a significant predictor of daily movement during the summer in Pine Valley, temporal constancy functioned to significantly reduce the positive effect of spatial constancy on daily movement in this seasonal environment. Individuals who inhabited spatially predictable home ranges

that were also highly temporally predictable (Figure 8, individual b) moved less per day than individuals whose home range was spatially, but not temporally predictable (Figure 8, individual a). As both spatial and temporal predictability increase, maximum theoretical environmental predictability is approached (Figure 3c). Our finding that spatial and temporal constancy interact to inform movement in this limiting environment is important, as it indicates that variability of resources on the landscape may become a larger factor for movement decisions when conditions drop below a threshold of habitat quality.

These findings also have important implications when considering human-caused environmental change. Changes in precipitation and temperature are impacting mountainous regions, where plant phenology and resource availability is linked closely to snow dynamics (IPCC Working Group, 2007; Post & Forchhammer, 2008; Stien et al., 2010), and causing low elevation, water-limited systems to become even more arid (Cayan et al., 2010; Seager et al., 2007; MacDonald, 2010; McLaughlin et al., 2017). In addition, human-development and use of wildlands occurs predominantly in lower-elevation areas (Haggerty et al., 2018; Polfus & Krausman, 2012) concurrent with winter ranges of temperate ungulates such as mule deer, and often cluster around vital water sources (Polfus & Krausman, 2012). As climate change, land-use change, and unfavorable vegetation succession shift the quality, predictability, and availability of food resources in these seasonal environments (Root et al., 2003; Svenning & Sandel, 2013), the efficacy and efficiency of these regionally tuned foraging tactics may vary (Roese et al., 1991), which could impact the energy balance, time budget, individual fitness, and population demographics of foraging ungulates.

Small differences in forage quality can have disproportionate influence on individual body condition and overwinter survival of ungulates (e.g. “multiplier effects”) (Cook et al., 2004; White, 1983; Bender et al., 2007), and shifts in forage quality and predictability may be especially impactful for mule deer, who are more selective than other ungulates in regard to nutrient and biomass constraints (Collins & Urness, 1983; Cox et al., 2009; Wallmo et al., 1977). This selectivity has the potential to reduce the carrying capacity of mule deer seasonal habitats by increasing space requirements of foraging individuals (Rivrud et al., 2019; Stephens & Krebs, 1986; Pastor et al., 1997) or causing individuals to switch movement tactics (Robb et al, 2019). An additional consideration is behavioral and physiological thermoregulation costs associated with a changing climate (Aublet et al., 2009; Sears & Angilletta, 2015), which could compound energetic costs of foraging if increased movement is required to meet nutritional requirements under new seasonal dynamics. As foraging energetics at the individual level are documented to scale up to impact population parameters of mule deer (Heffelfinger, 2006; Monteith et al., 2014), shifts in predictability could impact population viability (Post, 2005).

Changes to forage quality and landscape predictability can impact ungulates' fitness in other ways. Deer have been found to forage for longer when forage availability (Parker et al., 2009) and quality (Wilmshurst et al., 1995) is lower, which may increase their vulnerability to predation and hunting (Lima & Bednekoff, 1999; Loudon et al., 1983), and landscape heterogeneity – which may be altered by both climate change and human development – is also well documented to moderate predator prey interactions (Gorini et al., 2011; Altendorf et al., 2001; Proffitt et al., 2009). In addition, reductions in environmental predictability due to a changing climate may make anthropogenic resources (e.g., cropland, irrigated lawns) more attractive, resulting in increased residence of ungulates near human development (Barker et al., 2019; Robb et al., 2019). Greater animal density in proximity to human development may increase rates of human-wildlife conflict such as crop depredation and wildlife-vehicle collisions, which are costly and impact the welfare of humans and wildlife alike (Gill et al., 1992; Bissonette et al., 2008; Sawyer et al., 2016).

If ungulate populations are unable to adapt to these human-driven impacts due to low plasticity in their movement behavior, landscape changes may have highly negative individual fitness and population-level consequences (Robertson et al., 2013). Relative to other ungulate species, mule deer have demonstrated low behavioral plasticity in regard to migratory propensity (Sawyer et al., 2019) and have high site (Morrison et al., 2021) and route fidelity even to areas that have experienced human development (Wyckoff et al., 2018), which may indicate their vulnerability to rapid environmental change. As the American Southwest is projected to experience substantial impacts from climate change (Dillon et al., 2016; Walther et al., 2002; Watkins et al., 2007; Field & Barros, 2014) and is currently observing high rates of human population growth and development expansion (Hansen et al., 2014), understanding how mule deer move in response to dynamic resource landscapes is crucial for their conservation and management.

Mule deer are a cosmopolitan species with a wide distribution, covering many habitat types and climatic zones and the two populations examined here offer an interesting contrast. While it is easy to conceive that spatial and temporal constancy of resources would reduce organisms' need to move, I have identified that vegetation predictability leads to greater movement when interacting with certain home range and ecosystem qualities. Our results emphasize the importance of considering ecological context when examining drivers of animal movement and highlight the role of environmental predictability in informing unique, fine-scale movement tactics.

Here I have focused on small scale movement in the context of individual home range-scale vegetation predictability. Our work underscores the utility of forage constancy as a quantitative metric driving animal movement at both large *and* small scales and emphasize the need to consider ecological context by studying species'

response to dynamic resource landscapes at the population level and in a seasonal context. In this study I calculated average environmental predictability over the course of a site-specific season and examined it in the context of mean daily distance traveled within that season. I urge future research to relate home range predictability to quantitative metrics of animal fitness (e.g., fat gain) and build on this work by conducting temporally and spatially explicit analyses to understand how inter-season predictability dynamics and landscape configuration direct patterns of animal movement and space use.

Spatial predictability likely changes over the course of the season as plant quality shifts (Van Soest, 2018), and vegetation composition may mediate these dynamics. In landscapes with herbaceous forage, vegetation greenness is more dynamic within a season and responds quickly to rain events whereas shrub-dominated landscapes are more stable over time in regard to NDVI (Moreno-De Las Heras et al., 2015). Examining if changes in spatial predictability through time drive temporal patterns in individual daily movement and space use could help us identify periods where climate events (e.g., drought, fires, rain) may be most impactful for moving animals. Additionally, if specific vegetative assemblages are associated with stable spatial predictability, habitat restoration efforts can be targeted to promote these assemblages.

Animals' use of environmental predictability as a source of environmental information may also change over time. For migrating ungulates, Bauer et al (2020) determined that predictability along different sections of the migration route was not equally important in dictating timing of relocations and fitness outcomes. Determining how the effect of predictability on movement shifts over the course of the year or season will further elucidate how climate events and general climate change may impact ungulate populations.

Finally, during this analysis I did not examine NDVI values in a spatially explicit manner (i.e., examining clustering or dispersion of values). Calculating temporal constancy in conjunction with spatial structure (e.g., using Moran's I to determine if temporally predictable locations are clustered in space) would help disentangle the effects of forage availability and spatial configuration on daily relocation decisions.

Conclusion

Linking movement to environmental drivers is a complex task. Movement strategies are variably expressed within ecosystems (Jonzén et al., 2011) and available forage is only one of several habitat considerations for moving animals. Unexplained variance in daily movement is likely results from additional environmental factors such as water availability (Woods et al., 2001), human development (Lendrum et al., 2012), presence of pests (Johnson et al., 2021), and

predation risk (Latombe et al., 2014). Other factors impacting ungulate movement include intra- and inter-specific (Johnson et al., 2000) interactions and time-specific energetic cost of specific life-history stages (Long et al., 2009). These factors are numerous and interacting and complicate our ability to isolate and identify movement patterns resulting from predictability of forage resources.

Additionally, understanding the role of environmental predictability in animal movement ecology is complicated by feedbacks between movement causes and consequences. Predictability plays a primary role in the evolution of movement-related abilities and establishment of relocation tactics and in turn, these traits and behaviors determine if environmental predictability is perceived, how and if it is utilized, and the environments and locations used by an organism. Simply put, movement directed by environmental predictability influences the amount of predictability experienced, creating an "experiential niche" (Snell-Rood & Steck, 2019; Shaw, 2020).

Understanding how environmental predictability informs movement behavior at multiple scales is fundamental to the fields of movement ecology and animal behavior and is important for wildlife conservation and management in our increasingly changing world. Mule deer populations have declined sharply in the 1990s, but the factors contributing to this decline are disputed and remain largely unknown (Heffelfinger & Messmer, 2003; Heffelfinger, 2006; Unsworth et al., 1999; Bergman et al., 2015). Our findings link environmental predictability and mule deer movement and may represent an important mechanism driving population demographics. Maintenance of seasonal movement and space use of large ungulates such as mule deer is extremely crucial, as these behaviors impact the health and functioning of larger communities, and ecosystem processes (Bauer & Hoye, 2014; Frank, 1998; Shaw, 2020).

Literature Cited

Abrahms, B., Aikens, E. O., Armstrong, J. B., Deacy, W. W., Kauffman, M. J., & Merkle, J. A. (2021). Emerging perspectives on resource tracking and animal movement ecology. *Trends in Ecology & Evolution*, *36*(4), 308-320.

Abrahms, B., Hazen, E. L., Aikens, E. O., Savoca, M. S., Goldbogen, J. A., Bograd, S. J., ... & Mate, B. R. (2019). Memory and resource tracking drive blue whale migrations. *Proceedings of the National Academy of Sciences*, *116*(12), 5582-5587.

Aikens, E. O., Mysterud, A., Merkle, J. A., Cagnacci, F., Rivrud, I. M., Hebblewhite, M., ... & Kauffman, M. J. (2020). Wave-like patterns of plant phenology determine ungulate movement tactics. *Current Biology*, *30*(17), 3444-3449.

Albon, S. D., & Langvatn, R. (1992). Plant phenology and the benefits of migration in a temperate ungulate. *Oikos*, 502-513.

Altendorf, K. B., Laundré, J. W., López González, C. A., & Brown, J. S. (2001). Assessing effects of predation risk on foraging behavior of mule deer. *Journal of mammalogy*, *82*(2), 430-439.

Aublet, J. F., Festa-Bianchet, M., Bergero, D., & Bassano, B. (2009). Temperature constraints on foraging behaviour of male Alpine ibex (Capra ibex) in summer. *Oecologia*, *159*, 237-247.

Avgar, T., Mosser, A., Brown, G. S., & Fryxell, J. M. (2013). Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *Journal of Animal Ecology*, *82*(1), 96-106.

Baharav, D., & Rosenzweig, M. L. (1985). Optimal foraging in Dorcas gazelles. *Journal of arid environments*, *9*(2), 167-171.

Banner, R. E. (1992). Vegetation types of Utah.

Barker, K. J., Mitchell, M. S., & Proffitt, K. M. (2019). Native forage mediates influence of irrigated agriculture on migratory behaviour of elk. *Journal of Animal Ecology*, *88*(7), 1100-1110.

Bastille-Rousseau, G., Gibbs, J. P., Yackulic, C. B., Frair, J. L., Cabrera, F., Rousseau, L. P., ... & Blake, S. (2017). Animal movement in the absence of predation: environmental drivers of movement strategies in a partial migration system. *Oikos*, *126*(7), 1004-1019.

Bates D, Mächler M, Bolker B, Walker S (2015). "Fitting Linear Mixed-Effects Models Using lme4." Journal of Statistical Software, 67(1), 1–48. doi:10.18637/jss.v067.i01.

Bauer, S., McNamara, J. M., & Barta, Z. (2020). Environmental variability, reliability of information and the timing of migration. *Proceedings of the Royal Society B*, *287*(1926), 20200622.

Bauer, S., & Hoye, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, *344*(6179).

Bautista, C., Oeser, J., Kuemmerle, T., & Selva, N. (2023). Resource pulses and human–wildlife conflicts: linking satellite indicators and ground data on forest productivity to predict brown bear damages. *Remote Sensing in Ecology and Conservation*, *9*(1), 90-103.

Bender, L. C., Lomas, L. A., & Browning, J. (2007). Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. *The Journal of Wildlife Management*, *71*(4), 1118-1124.

Benhamou, S. (2014). Of scales and stationarity in animal movements. *Ecology letters*, *17*(3), 261-272.

Bergman, E. J., Doherty Jr, P. F., White, G. C., & Holland, A. A. (2015). Density dependence in mule deer: a review of evidence. *Wildlife Biology*, *21*(1), 18-29.

Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Van Moorter, B., & Mysterud, A. (2012). A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave?. *The American Naturalist*, *180*(4), 407-424.

Bishop, C. J., White, G. C., Freddy, D. J., Watkins, B. E., & Stephenson, T. R. (2009). Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs*, *172*(1), 1-28.

Bissonette, J. A., Kassar, C. A., & Cook, L. J. (2008). Assessment of costs associated with deer–vehicle collisions: human death and injury, vehicle damage, and deer loss. *Human-Wildlife Conflicts*, *2*(1), 17-27.

Bolger, D. T., Newmark, W. D., Morrison, T. A., & Doak, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology letters*, *11*(1), 63-77.

Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology letters*, *11*(6), 637-650.

Bowman, A. W. (1985). A comparative study of some kernel-based nonparametric density estimators. *Journal of Statistical Computation and Simulation*, *21*(3-4), 313-327.

Bowyer, R. T., Kie, J. G., & Van Ballenberghe, V. (1998). Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation?. *Journal of Mammalogy*, *79*(2), 415-425.

Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modeling*, 197, 516-519

Cayan, D. R., Das, T., Pierce, D. W., Barnett, T. P., Tyree, M., & Gershunov, A. (2010). Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences*, *107*(50), 21271-21276.

Collins, W. B., & Urness, P. J. (1983). Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. *The Journal of Wildlife Management*, 646-663.

Colwell, R. K. (1974). Predictability, constancy, and contingency of periodic phenomena. *Ecology*, *55*(5), 1148-1153.

Cook, J. G., Johnson, B. K., Cook, R. C., Riggs, R. A., Delcurto, T. I. M., Bryant, L. D., & Irwin, L. L. (2004). Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife monographs*, *155*(1), 1-61.

Couriot, O., Hewison, A. M., Saïd, S., Cagnacci, F., Chamaillé-Jammes, S., Linnell, J. D., ... & Morellet, N. (2018). Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore. *Oecologia*, *187*, 47-60.

Cox, M., D. W. Lutz, T. Wasley, M. Fleming, B. B. Compton, T. Keegan, D. Stroud, S. Kilpatrick, K. Gray, J. Carlson, L. Carpenter, K. Urquhart, B. Johnson, and C. McLaughlin. (2009). Habitat Guidelines for Mule Deer: Intermountain West Ecoregion. *Mule Deer Working Group, Western Association of Fish and Wildlife Agencies*

Cox, S. [image]. Agricultural Research Center. U.S. Department of Agriculture. https://www.ars.usda.gov/oc/images/photos/feb06/d423-1/

Crook, D. A., Buckle, D. J., Morrongiello, J. R., Allsop, Q. A., Baldwin, W., Saunders, T. M., & Douglas, M. M. (2020). Tracking the resource pulse: Movement responses of fish to dynamic floodplain habitat in a tropical river. *Journal of Animal Ecology*, *89*(3), 795-807.

Dailey, T. V., & Hobbs, N. T. (1989). Travel in alpine terrain: energy expenditures for locomotion by mountain goats and bighorn sheep. *Canadian Journal of Zoology*, *67*(10), 2368-2375.

Dillon, M. E., Woods, H. A., Wang, G., Fey, S. B., Vasseur, D. A., Telemeco, R. S., ... & Pincebourde, S. (2016). Life in the frequency domain: the biological impacts of changes in climate variability at multiple time scales. *Integrative and comparative biology*, *56*(1), 14-30.

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, *70*(4).

Esmaeili, S., Jesmer, B. R., Albeke, S. E., Aikens, E. O., Schoenecker, K. A., King, S. R., ... & Goheen, J. R. (2021). Body size and digestive system shape resource selection by ungulates: A cross-taxa test of the forage maturation hypothesis. *Ecology letters*, *24*(10), 2178-2191.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., ... & Mueller, T. (2013). Spatial memory and animal movement. *Ecology letters*, *16*(10), 1316-1329.

Fancy, S. G., & White, R. G. (1987). Energy expenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology*, *65*(1), 122-128.

Ferguson, S. H., Taylor, M. K., Born, E. W., Rosing-Asvid, A., & Messier, F. (1999). Determinants of home range size for polar bears (Ursus maritimus). *Ecology letters*, *2*(5), 311-318.

Field, C. B., & Barros, V. R. (Eds.). (2014). *Climate Change 2014–Impacts, Adaptation and Vulnerability: Global and Sectoral Aspects*. Cambridge University Press.

Frank, D. A. (1998). Ungulate regulation of ecosystem processes in Yellowstone National Park: direct and feedback effects. *Wildlife Society Bulletin*, *26*(3), 410-418.

Fronhofer, E. A., Hovestadt, T., & Poethke, H. J. (2013). From random walks to informed movement. *Oikos*, *122*(6), 857-866.

Fryxell, J. M. (1991). Forage quality and aggregation by large herbivores. *The American Naturalist*, *138*(2), 478-498.

Fryxell, J. M., & Sinclair, A. R. E. (1988). Causes and consequences of migration by large herbivores. *Trends in ecology & evolution*, *3*(9), 237-241.

Fryxell, J. M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., ... & Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National academy of Sciences*, *105*(49), 19114-19119.

Garrott, R. A., White, G. C., Bartmann, R. M., Carpenter, L. H., & Alldredge, A. W. (1987). Movements of female mule deer in northwest Colorado. *The Journal of Wildlife Management*, 634-643.

Geist, V. (1981). Behavior: adaptive strategies in mule deer. *Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA*, 157-223.

Gilbert, S. L., Hundertmark, K. J., Person, D. K., Lindberg, M. S., & Boyce, M. S. (2017). Behavioral plasticity in a variable environment: snow depth and habitat interactions drive deer movement in winter. *Journal of Mammalogy*, *98*(1), 246-259.

Gill, R. M. A. (1992). A review of damage by mammals in north temperate forests: 1. Deer. *Forestry: An International Journal of Forest Research*, *65*(2), 145-169.

Giralt-Rueda, J. M., & Santamaría, L. (2023). Landscape heterogeneity increases the stability of wild ungulate populations facing climatic variability in Mediterranean ecosystems. *Science of The Total Environment*, 164826.

Goodson, N. J., Stevens, D. R., & Bailey, J. A. (1991). Effects of snow on foraging ecology and nutrition of bighorn sheep. *The Journal of wildlife management*, 214-222.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone.

Gorini, L., Linnell, J. D., May, R., Panzacchi, M., Boitani, L., Odden, M., & Nilsen, E. B. (2011). Habitat heterogeneity and mammalian predator–prey interactionsmam_189 55.. 77. *Mammal review*, *42*(1), 55-77.

Haggerty, J. H., Epstein, K., Stone, M., & Cross, P. C. (2018). Land use diversification and intensification on elk winter range in Greater Yellowstone: Framework and agenda for social-ecological research. *Rangeland Ecology & Management*, *71*(2), 171-174.

Hamel, S., Garel, M., Festa-Bianchet, M., Gaillard, J. M., & Côté, S. D. (2009). Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *Journal of Applied Ecology*, *46*(3), 582-589.

Hanley, T. A. (1997). A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). *Oikos*, 209-218.

Hansen, A. J., Piekielek, N., Davis, C., Haas, J., Theobald, D. M., Gross, J. E., ... & Running, S. W. (2014). Exposure of US National Parks to land use and climate change 1900–2100. *Ecological Applications*, *24*(3), 484-502.

Hanser, S. [image]. Sagebrush in the Great Basin, UT. USGS. https://www.usgs.gov/media/images/sagebrush-great-basin-ut

Hebblewhite, M., & Merrill, E. H. (2009). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, *90*(12), 3445-3454.

Hebblewhite, M., Merrill, E., & McDermid, G. (2008). A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological monographs*, *78*(2), 141-166.

Heffelfinger, J. (2006). *Deer of the Southwest: a complete guide to the natural history, biology, and management of southwestern mule deer and white-tailed deer*. Texas A&M University Press.

Heffelfinger, J.R., & Messmer, T.A. (2003). Introduction In: deVos, J.C., Jr., Conover, M.R. & Headrick, N.E. (Eds.); Mule deer conservation: Issues and management strategies. Berryman Institute Press, Utah State University, Logan, Utah, USA, pp. 1-11.

Hehman, M. W., & Fulbright, T. E. (1997). Use of warm-season food plots by white-tailed deer. *The Journal of wildlife management*, 1108-1115.

Hervert, J. J., & Krausman, P. R. (1986). Desert mule deer use of water developments in Arizona. *The Journal of wildlife management*, 670-676.

Hudson, R. J., Haigh, J. C., & Bubenik, A. B. (2002). Physical and physiological adaptations. *North American elk: ecology and management. Smithsonian Institution Press, Washington, DC*, 199-257.

Hurley, M. A., Hebblewhite, M., Gaillard, J. M., Dray, S., Taylor, K. A., Smith, W. K., ... & Bonenfant, C. (2014). Functional analysis of normalized difference vegetation index curves reveals overwinter mule deer survival is driven by both spring and autumn

phenology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1643), 20130196.
IPCC Working Group I. (2007). IPCC fourth assessment report. United Nations Intergovernmental Panel on Climate Change, Geneva, Switzerland.
Jacques, C. N., Jenks, J. A., Deperno, C. S., Sievers, J. D., Grovenburg, T. W., Brinkman, T. J., ... & Stillings, B. A. (2009). Evaluating ungulate mortality associated with helicopter net-gun captures in the Northern Great Plains. *The Journal of Wildlife Management*, *73*(8), 1282-1291.
Johnson, B. K., Kern, J. W., Wisdom, M. J., Findholt, S. L., & Kie, J. G. (2000). Resource selection and spatial separation of mule deer and elk during spring. *The Journal of Wildlife Management*, 685-697.
Johnson, H. E., Golden, T. S., Adams, L. G., Gustine, D. D., Lenart, E. A., & Barboza, P. S. (2021). Dynamic selection for forage quality and quantity in response to phenology and insects in an Arctic ungulate. *Ecology and Evolution*, *11*(17), 11664-11688.
Joly, K., Gurarie, E., Hansen, D. A., & Cameron, M. D. (2021). Seasonal patterns of spatial fidelity and temporal consistency in the distribution and movements of a migratory ungulate. *Ecology and Evolution*, *11*(12), 8183-8200.
Jonzén, N., Knudsen, E., Holt, R. D., & Sæther, B. E. (2011). Uncertainty and predictability: the niches of migrants and nomads. *Animal migration: a synthesis*, *91*, 109.
Kie, J. G. (1999). Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy*, *80*(4), 1114-1129.
Krahulec, K. [image]. The Uinta Mountains: A Tale of Two Geographies and More. Utah Geological Survey. https://geology.utah.gov/map-pub/survey-notes/uinta-mountains-two-geographies/#toggle-id-1
Kranstauber, B., Smolla, M., & Scharf, A. (2021). move: Visualizing and Analyzing Animal Track Data. R package version 4.1.6, https://CRAN.R-project.org/package=move.
Latombe, G., Fortin, D., & Parrott, L. (2014). Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology*, *83*(1), 185-198.
Lendrum, P. E., Anderson Jr, C. R., Long, R. A., Kie, J. G., & Bowyer, R. T. (2012). Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. *Ecosphere*, *3*(9), 1-19.
Lesage, L., Crête, M., Huot, J., & Ouellet, J. P. (2001). Evidence for a trade-off between growth and body reserves in northern white-tailed deer. *Oecologia*, *126*, 30-41.
Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist*, *153*(6), 649-659.
Long, R. A., Kie, J. G., Terry Bowyer, R., & Hurley, M. A. (2009). Resource selection and movements by female mule deer Odocoileus hemionus: effects of reproductive stage. *Wildlife Biology*, *15*(3), 288-298.
Loudon, A. S., McNeilly, A. S., & Milne, J. A. (1983). Nutrition and lactational control of fertility in red deer. *Nature*, *302*(5904), 145-147.
MacDonald, G. M. (2010). Water, climate change, and sustainability in the southwest. *Proceedings of the National Academy of Sciences*, *107*(50), 21256-21262.
Manser, M. B., & Brotherton, P. N. M. (1995). Environmental constraints on the foraging behaviour of a dwarf antelope (Madoqua kirkii). *Oecologia*, *102*, 404-412.
Marshal, J. P., Krausman, P. R., & Bleich, V. C. (2005). Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. *Rangeland Ecology & Management*, *58*(4), 360-365.
Martin, J., Benhamou, S., Yoganand, K., & Owen-Smith, N. (2015). Coping with spatial heterogeneity and temporal variability in resources and risks: adaptive movement behaviour by a large grazing herbivore. *PloS one*, *10*(2), e0118461.
McKinney, T. 2003. Precipitation, weather, and mule deer. Pages 219–237 in J. C. deVos, Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Press, Logan, Utah, USA.
McLaughlin, B. C., Ackerly, D. D., Klos, P. Z., Natali, J., Dawson, T. E., & Thompson, S. E. (2017). Hydrologic refugia, plants, and climate change. *Global change biology*, *23*(8), 2941-2961.

McPeek, M. A., & Holt, R. D. (1992). The evolution of dispersal in spatially and temporally varying environments. *The American Naturalist*, *140*(6), 1010-1027.

Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., ... & Kauffman, M. J. (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1833), 20160456.

Mery, F. (2013). Natural variation in learning and memory. *Current opinion in neurobiology*, *23*(1), 52-56.

Middleton, A. D., Merkle, J. A., McWhirter, D. E., Cook, J. G., Cook, R. C., White, P. J., & Kauffman, M. J. (2018). Green-wave surfing increases fat gain in a migratory ungulate. *Oikos*, *127*(7), 1060-1068.

Moeslund, J. E., Arge, L., Bøcher, P. K., Dalgaard, T., & Svenning, J. C. (2013). Topography as a driver of local terrestrial vascular plant diversity patterns. *Nordic Journal of Botany*, *31*(2), 129-144.

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Kie, J. G., & Bowyer, R. T. (2014). Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs*, *186*(1), 1-62.

Monteith, K. L., Bleich, V. C., Stephenson, T. R., Pierce, B. M., Conner, M. M., Klaver, R. W., & Bowyer, R. T. (2011). Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere*, *2*(4), 1-34.

Montgomery, R. A., Redilla, K. M., Ortiz-Calo, W., Smith, T., Keller, B., & Millspaugh, J. J. (2018). Evaluating the individuality of animal-habitat relationships. *Ecology and Evolution*, *8*(22), 10893-10901.

Moorcroft, P. R., & Lewis, M. A. (2013). Mechanistic home range analysis.(MPB-43). In *Mechanistic Home Range Analysis.(MPB-43)*. Princeton University Press.

Morales, J. M., Fortin, D., Frair, J. L., & Merrill, E. H. (2005). Adaptive models for large herbivore movements in heterogeneous landscapes. *Landscape Ecology*, *20*, 301-316.

Morand-Ferron, J., Cole, E. F., & Quinn, J. L. (2016). Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biological Reviews*, *91*(2), 367-389.

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., ... & Mysterud, A. (2013). Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, *82*(6), 1326-1339.

Moreno-De Las Heras, M., Díaz-Sierra, R., Turnbull, L., & Wainwright, J. (2015). Assessing vegetation structure and ANPP dynamics in a grassland–shrubland Chihuahuan ecotone using NDVI–rainfall relationships. *Biogeosciences*, *12*(10), 2907-2925.

Morrison, T. A., Merkle, J. A., Hopcraft, J. G. C., Aikens, E. O., Beck, J. L., Boone, R. B., ... & Kauffman, M. J. (2021). Drivers of site fidelity in ungulates. *Journal of animal ecology*, *90*(4), 955-966.

Mueller, T., and W. F. Fagan. 2008. Search and navigation in dynamic environments - from individual behaviours to population distributions. Oikos 117:654–664.

Mueller, T., Olson, K.A., Dressler, G., Leimgruber, P., Fuller, T.K., Nicolson, C., Novaro, A.J., Bolgeri, M.J., Wattles, D., DeStefano, S., Calabrese, J.M. & Fagan, W.F. (2011) How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography, 20, 683–694.

Murden, S. B., & Risenhoover, K. L. (1993). Effects of habitat enrichment on patterns of diet selection. *Ecological Applications*, *3*(3), 497-505.

Murray, M. G. (1991). Maximizing energy retention in grazing ruminants. *The Journal of Animal Ecology*, 1029-1045.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in ecology and evolution*, *4*(2), 133-142.

Nandintsetseg, D., Bracis, C., Leimgruber, P., Kaczensky, P., Buuveibaatar, B., Lkhagvasuren, B., ... & Mueller, T. (2019). Variability in nomadism: environmental gradients modulate the movement behaviors of dryland ungulates. *Ecosphere*, *10*(11), e02924.

Nandintsetseg, D., Kaczensky, P., Ganbaatar, O., Leimgruber, P., & Mueller, T. (2016). Spatiotemporal habitat dynamics of ungulates in unpredictable environments: The khulan

(Equus hemionus) in the Mongolian Gobi desert as a case study. *Biological Conservation*, *204*, 313-321.

Neumann, W., Martinuzzi, S., Estes, A. B., Pidgeon, A. M., Dettki, H., Ericsson, G., & Radeloff, V. C. (2015). Opportunities for the application of advanced remotely-sensed data in ecological studies of terrestrial animal movement. *Movement ecology*, *3*, 1-13.

Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annual review of ecology and systematics*, *4*(1), 25-51.

NPS [image]. Pinyon Juniper Woodlands. https://www.nps.gov/para/learn/nature/pinyon-juniper-woodlands.htm

Ogutu, J. O., Piepho, H. P., & Dublin, H. T. (2014). Responses of phenology, synchrony and fecundity of breeding by African ungulates to interannual variation in rainfall. *Wildlife Research*, *40*(8), 698-717.

Omernik, J.M. (1987). Ecoregions of the conterminous United States. Map (scale 1:7,500,000). *Annals of the Association of American Geographers*. 77(1), 118-125.

Omernik, J.M.(1995). Ecoregions: A spatial framework for environmental management. In: Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making. Davis, W.S. and T.P. Simon (eds.), Lewis Publishers, Boca Raton, FL. p. 49-62.

Owen-Smith, N. (1994). Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology*, *75*(4), 1050-1062.

Owen-Smith, N. (2013). Daily movement responses by African savanna ungulates as an indicator of seasonal and annual food stress. *Wildlife Research*, *40*(3), 232-240.

Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. (2010). Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1550), 2267-2278.

Parker, K. L., Barboza, P. S., & Gillingham, M. P. (2009). Nutrition integrates environmental responses of ungulates. *Functional ecology*, *23*(1), 57-69.

Parker, K. L., Robbins, C. T., & Hanley, T. A. (1984). Energy expenditures for locomotion by mule deer and elk. *The Journal of Wildlife Management*, 474-488.

Passadore, C., Möller, L., Diaz-Aguirre, F., & Parra, G. J. (2018). High site fidelity and restricted ranging patterns in southern Australian bottlenose dolphins. *Ecology and evolution*, *8*(1), 242-256.

Pastor, J., Moen, R., & Cohen, Y. (1997). Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. *Journal of Mammalogy*, *78*(4), 1040-1052.

Peters, W., Hebblewhite, M., Mysterud, A., Eacker, D., Hewison, A. M., Linnell, J. D., ... & Cagnacci, F. (2019). Large herbivore migration plasticity along environmental gradients in Europe: life-history traits modulate forage effects. *Oikos*, *128*(3), 416-429.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in ecology & evolution*, *20*(9), 503-510.

Pinheiro, J., & Bates, D. (2006). *Mixed-effects models in S and S-PLUS*. Springer science & business media.

Polfus, J. L., & Krausman, P. R. (2012). Impacts of residential development on ungulates in the Rocky Mountain West. *Wildlife Society Bulletin*, *36*(4), 647-657.

Post, E. (2005). Large-scale spatial gradients in herbivore population dynamics. *Ecology*, *86*(9), 2320-2328.

Post, E., & Forchhammer, M. C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1501), 2367-2373.

Proffitt, K. M., Grigg, J. L., Hamlin, K. L., & Garrott, R. A. (2009). Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *The Journal of Wildlife Management*, *73*(3), 345-356.

R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ramsey, R. D., & West, N. E. (2009). Vegetation of Utah. *Rangeland Resources of Utah*, 49-94.

Rautenstrauch, K. R., & Krausman, P. R. (1989). Influence of water availability and rainfall on movements of desert mule deer. *Journal of Mammalogy*, *70*(1), 197-201.

Riotte-Lambert, L., & Matthiopoulos, J. (2020). Environmental predictability as a cause and consequence of animal movement. *Trends in ecology & evolution*, *35*(2), 163-174.

Rivrud, I. M., Meisingset, E. L., Loe, L. E., & Mysterud, A. (2019). Future suitability of habitat in a migratory ungulate under climate change. *Proceedings of the Royal Society B*, *286*(1899), 20190442.

Robb, B., Huang, Q., Sexton, J. O., Stoner, D., & Leimgruber, P. (2019). Environmental Differences between Migratory and Resident Ungulates—Predicting Movement Strategies in Rocky Mountain Mule Deer (Odocoileus hemionus) with Remotely Sensed Plant Phenology, Snow, and Land Cover. *Remote Sensing*, *11*(17), 1980.

Robertson, B. A., Rehage, J. S., & Sih, A. (2013). Ecological novelty and the emergence of evolutionary traps. *Trends in ecology & evolution*, *28*(9), 552-560.

Robinson, B. G., & Merrill, E. H. (2012). The influence of snow on the functional response of grazing ungulates. *Oikos*, *121*(1), 28-34.

Roese, J. H., Risenhoover, K. L., & Folse, L. J. (1991). Habitat heterogeneity and foraging efficiency: an individual-based model. *Ecological modelling*, *57*(1-2), 133-143.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, *421*(6918), 57-60.

Ryan, S. J., Cross, P. C., Winnie, J., Hay, C., Bowers, J., & Getz, W. M. (2012). The utility of normalized difference vegetation index for predicting African buffalo forage quality. *The Journal of Wildlife Management*, *76*(7), 1499-1508.

Sæther, B. E. (1997). Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution*, *12*(4), 143-149.

Sand, H., Wikenros, C., Wabakken, P., & Liberg, O. (2006). Effects of hunting group size, snow depth and age on the success of wolves hunting moose. *Animal behaviour*, *72*(4), 781-789.

Sawyer, H., Merkle, J. A., Middleton, A. D., Dwinnell, S. P., & Monteith, K. L. (2019). Migratory plasticity is not ubiquitous among large herbivores. *Journal of Animal Ecology*, *88*(3), 450-460.

Sawyer, H., Middleton, A. D., Hayes, M. M., Kauffman, M. J., & Monteith, K. L. (2016). The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. *Ecosphere*, *7*(10), e01534.

Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A., Halpin, P.N., Joppa, L.N., McClellan, C.M. & Clark, J.S. (2008) Understanding movement data and movement processes: current and emerging directions.Ecology Letters, 11, 1338–1350.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103-113.

Schuler, K. L., Schroeder, G. M., Jenks, J. A., & Kie, J. G. (2014). Ad hoc smoothing parameter performance in kernel estimates of GPS-derived home ranges. *Wildlife Biology*, *20*(5), 259-266.

Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., ... & Naik, N. (2007). Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, *316*(5828), 1181-1184.

Sears, M. W., & Angilletta Jr, M. J. (2015). Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. *The American Naturalist*, *185*(4), E94-E102.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., & Swift, D. M. (1987). Large herbivore foraging and ecological hierarchies. *BioScience*, *37*(11), 789-799.

Shannon, C. E. (1948). A mathematical theory of communication. *The Bell system technical journal*, *27*(3), 379-423.

Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. *Movement ecology*, *8*(1), 12.

Shields, A. V., Larsen, R. T., & Whiting, J. C. (2012). Summer watering patterns of mule deer in the Great Basin Desert, USA: implications of differential use by individuals and the sexes for management of water resources. *The Scientific World Journal*, *2012*.

Signer, J., Fieberg, J., & Avgar, T. (2011). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution, 2019 9,880-890. URL https://doi.org/10.1002/ece3.4823.

Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary applications*, *4*(2), 367-387.
Sikes, R. S., Gannon, W. L., & Animal Care and Use Committee of the American Society of Mammalogists. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of mammalogy*, *92*(1), 235-253.
Snell-Rood, E. C., & Steck, M. K. (2019). Behaviour shapes environmental variation and selection on learning and plasticity: review of mechanisms and implications. *Animal Behaviour*, *147*, 147-156.
Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory* (Vol. 1). Princeton university press.
Stien, A., Loe, L. E., Mysterud, A., Severinsen, T., Kohler, J., & Langvatn, R. (2010). Icing events trigger range displacement in a high-arctic ungulate. *Ecology*, *91*(3), 915-920.
Stratmann, T. S., Forrest, M., Traylor, W., Dejid, N., Olson, K. A., Mueller, T., & Hickler, T. (2023). Movement drives population dynamics of one of the most mobile ungulates on Earth: Insights from a mechanistic model. *Ecology*, e4071.
Strickland, B. K., Hewitt, D. G., DeYoung, C. A., & Bingham, R. L. (2005). Digestible energy requirements for maintenance of body mass of white-tailed deer in southern Texas. *Journal of Mammalogy*, *86*(1), 56-60.
Svenning, J. C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, *100*(7), 1266-1286.
Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, *7*, 533-555.
Teitelbaum, C. S., & Mueller, T. (2019). Beyond migration: causes and consequences of nomadic animal movements. *Trends in Ecology & Evolution*, *34*(6), 569-581.
Tollefson, T. N., Shipley, L. A., Myers, W. L., Keisler, D. H., & Dasgupta, N. (2010). Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. *The Journal of wildlife management*, *74*(5), 974-986.
Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., & Lytle, D. A. (2017). Seasonality and predictability shape temporal species diversity. *Ecology*, *98*(5), 1201-1216.
Turner, M. G. (1989). Landscape ecology: the effect of pattern on process. *Annual review of ecology and systematics*, *20*(1), 171-197.
Turner, M. G., Pearson, S. M., Romme, W. H., & Wallace, L. L. (1997). Landscape heterogeneity and ungulate dynamics: what spatial scales are important?. In *Wildlife and landscape ecology: effects of pattern and scale* (pp. 331-348). New York, NY: Springer New York.
U.S. Environmental Protection Agency, 2000, Level III ecoregions of the continental United States (revision of Omernik, 1987): Corvallis, Oregon, U.S. Environmental Protection Agency-National Health and Environmental Effects Research Laboratory, Map M-1, various scales.
Unsworth, J. W., Pac, D. F., White, G. C., & Bartmann, R. M. (1999). Mule deer survival in Colorado, Idaho, and Montana. *The Journal of Wildlife Management*, 315-326.
Utah Division of Wildlife Resources, a. (2020). Deer Herd Unit Management Plan: Unit 8 (North Slope).
Utah Division of Wildlife Resources, b. (2020). Deer Herd Unit Management Plan: Unit 30 (Pine Valley).
Van de Kerk, M., McMillan, B. R., Hersey, K. R., Roug, A., & Larsen, R. T. (2020). Effect of net-gun capture on survival of mule deer. *The Journal of Wildlife Management*, *84*(4), 813-820.
Van Soest, P. J. (2018). *Nutritional ecology of the ruminant*. Cornell university press.
Viana, D. S., Granados, J. E., Fandos, P., Pérez, J. M., Cano-Manuel, F. J., Burón, D., ... & Soriguer, R. C. (2018). Linking seasonal home range size with habitat selection and movement in a mountain ungulate. *Movement Ecology*, *6*(1), 1-11.
WallisDeVries, M. F. (1996). Effects of resource distribution patterns on ungulate foraging behaviour: a modelling approach. *Forest Ecology and Management*, *88*(1-2), 167-177.
Wallmo, O. C., Carpenter, L. H., Regelin, W. L., Gill, R. B., & Baker, D. L. (1977). Evaluation of deer habitat on a nutritional basis.
Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., ... & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*(6879), 389-395.
Watkins, B. E., C. J. Bishop, E. J. Bergman, A. Bronson, B. Hale, B. F. Wakeling, L. H. Carpenter, and D. W. Lutz. (2007). Habitat guidelines for mule deer: Colorado Plateau shrubland and

forest ecoregion. Mule Deer Working Group, Western Association of Fish and Wildlife Agencies.

Weckerly, F. W. (1994). Selective feeding by black-tailed deer: forage quality or abundance?. *Journal of Mammalogy*, *75*(4), 905-913.

White, R. G. (1983). Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos*, 377-384.

Wickstrom, M. L., Robbins, C. T., Hanley, T. A., Spalinger, D. E., & Parish, S. M. (1984). Food intake and foraging energetics of elk and mule deer. *The Journal of wildlife management*, 1285-1301.

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional ecology*, *3*(4), 385-397.

Wilmshurst, J. F., Fryxell, J. M., & Hudsonb, R. J. (1995). Forage quality and patch choice by wapiti (Cervus elaphus). *Behavioral Ecology*, *6*(2), 209-217.

Woods, A.J., Lammers, D.A., Bryce, S.A., Omernik, J.M., Denton, R.L., Domeier, M., & Comstock, J.A. (2001). Ecoregions of Utah (color poster with map, descriptive text, summary tables, and photographs): Reston, Virginia, U.S. Geological Survey (map scale 1:1,175,000).

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, *70*(1), 164-168.

Wyckoff, T. B., Sawyer, H., Albeke, S. E., Garman, S. L., & Kauffman, M. J. (2018). Evaluating the influence of energy and residential development on the migratory behavior of mule deer. *Ecosphere*, *9*(2), e02113.

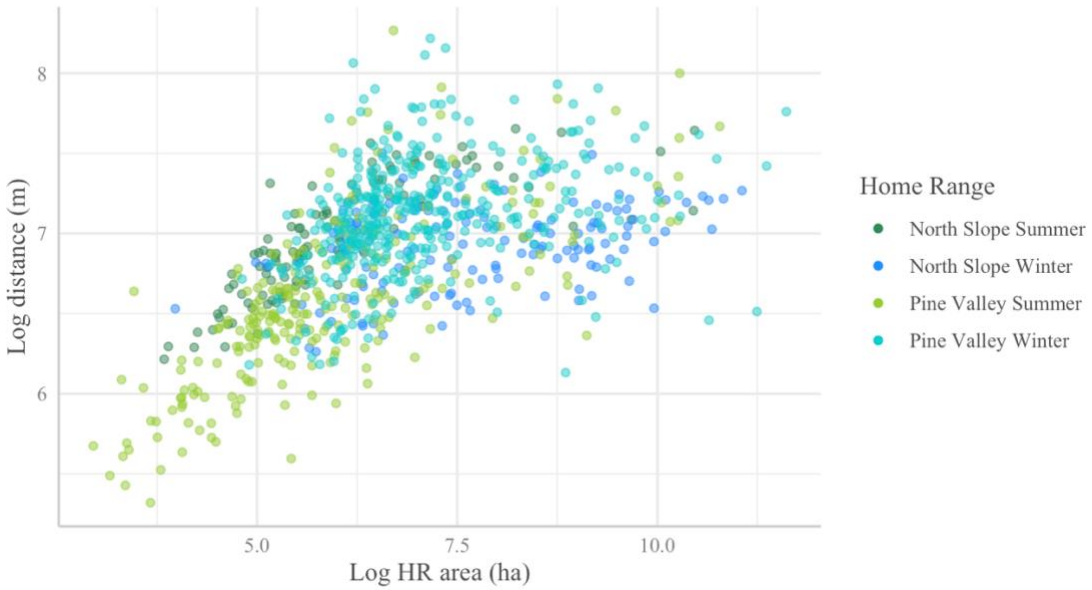
Supplemental Material

Supplementary Table 1 Spearman's correlation between number of animal fixes and home range area and daily distance.

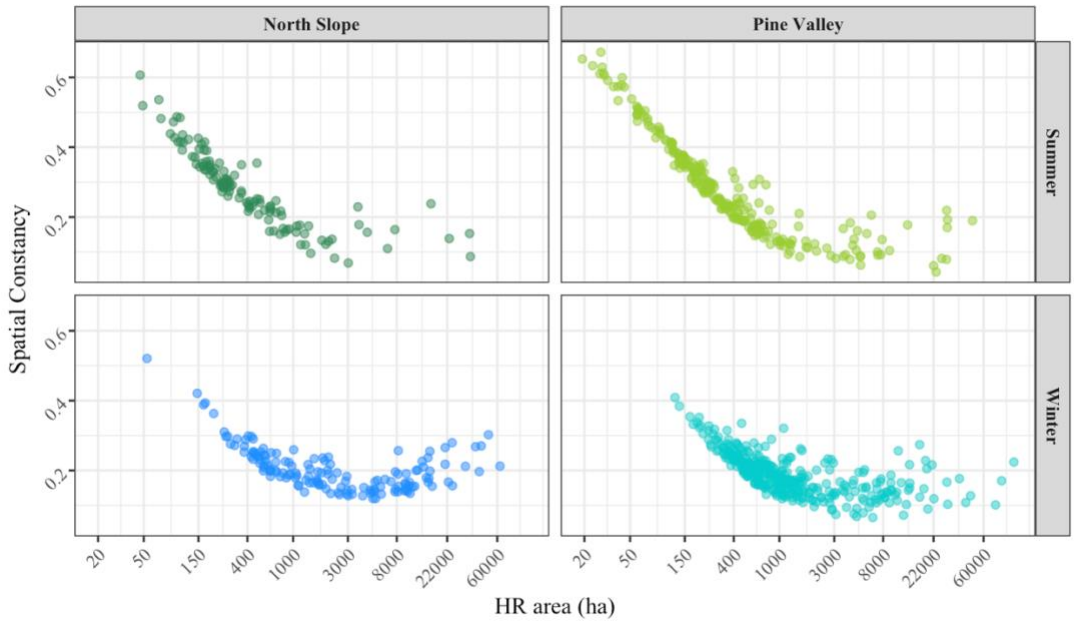
Range	*Daily Distance*	*HR Area*
North Slope Summer	-0.06384956	-0.02463621
North Slope Winter	0.199559	0.01244084
Pine Valley Summer	0.2213168	-0.1206117
Pine Valley Winter	0.3133888	0.06395287

Supplementary Table 2 Summary of season dates, fix numbers, unique seasons, and total number of seasonal home ranges included in analysis.

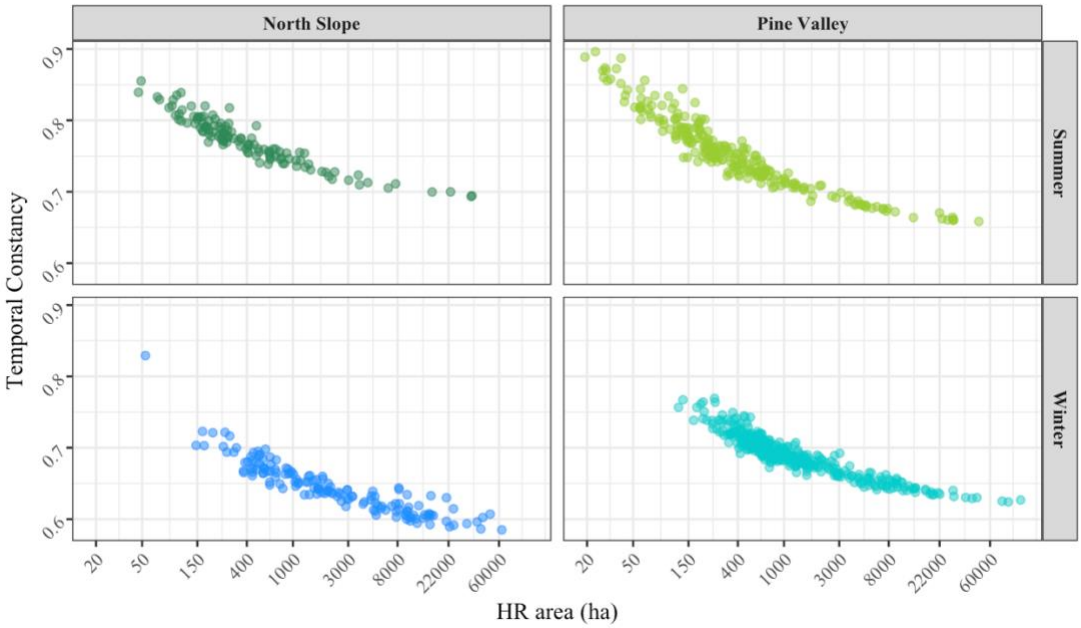
Range	*Julian*	*Calendar*	*Fixes (min // max)*	*Years // Unique Seasons*	*N*
North Slope Summer	170-260	Jun 19 – Sep 17	121 // 182	2018 – 2021 // 4	119
North Slope Winter	1-100 & 320-365	Jan 1 – Apr 10 & Nov 16 – Dec 31	192 // 294	2018 – 2022 // 4	151
Pine Valley Summer	140-250	May 20 – Sep 7	75 // 222	2016 – 2021 // 6	248
Pine Valley Winter	1-70 & 310-365	Jan 1 – Mar 11 & Nov 6 – Dec 31	91 // 254	2015 – 2022 // 7	362



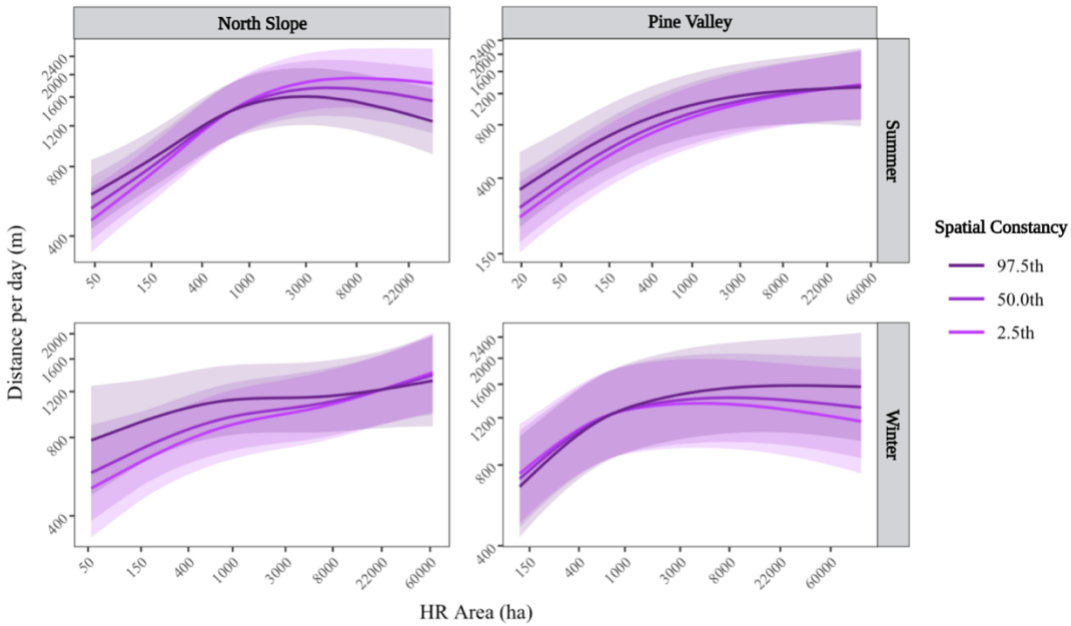
Supplementary Figure 1 Deer seasonal home range area (natural log scaled) and average distance traveled (natural log scaled).



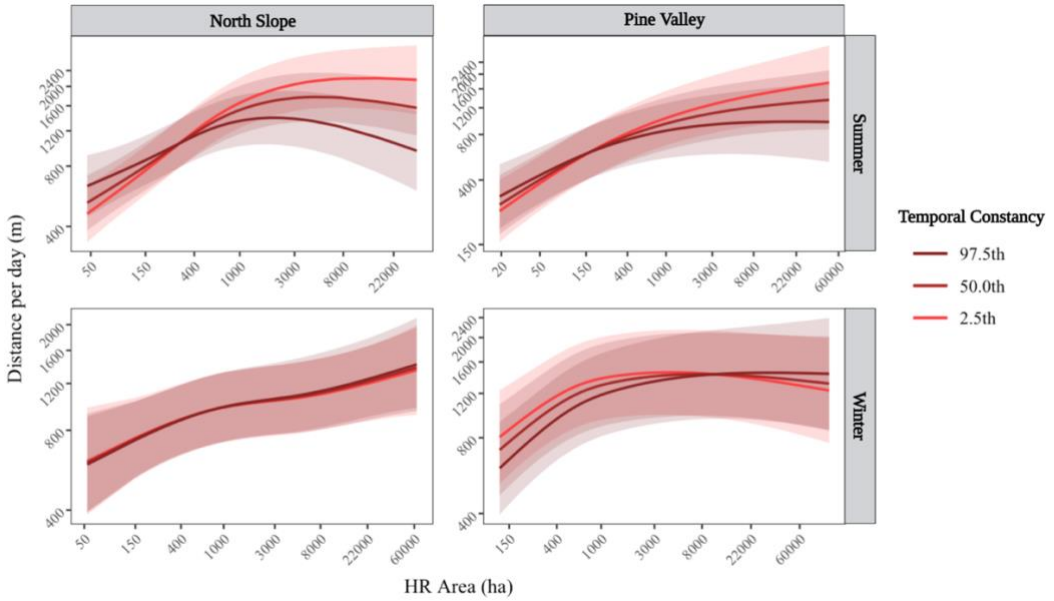
Supplementary Figure 2a Deer home range area and spatial constancy.



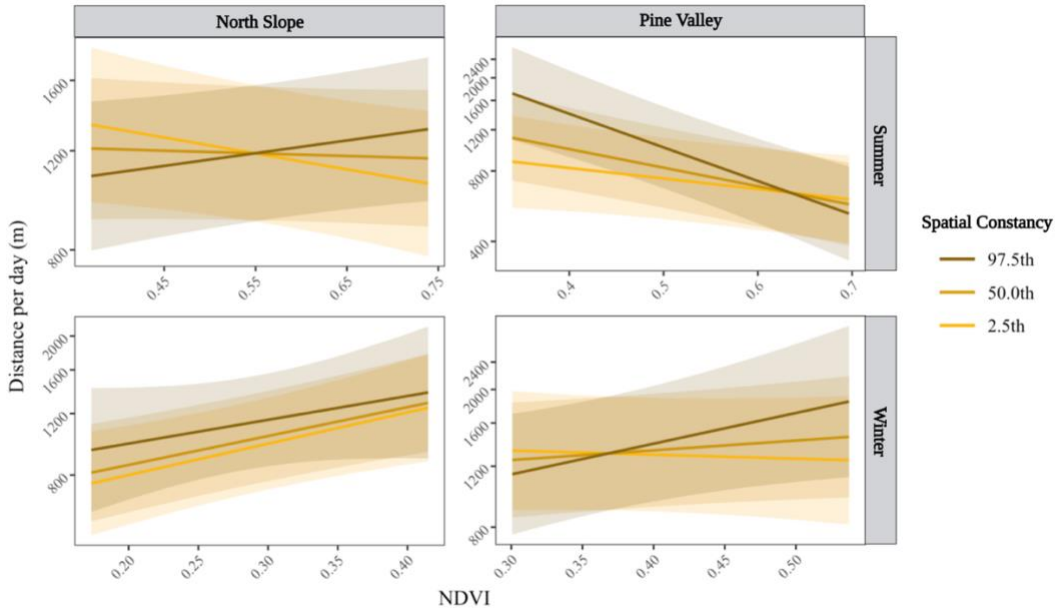
Supplementary Figure 2b Deer home range area and temporal constancy.



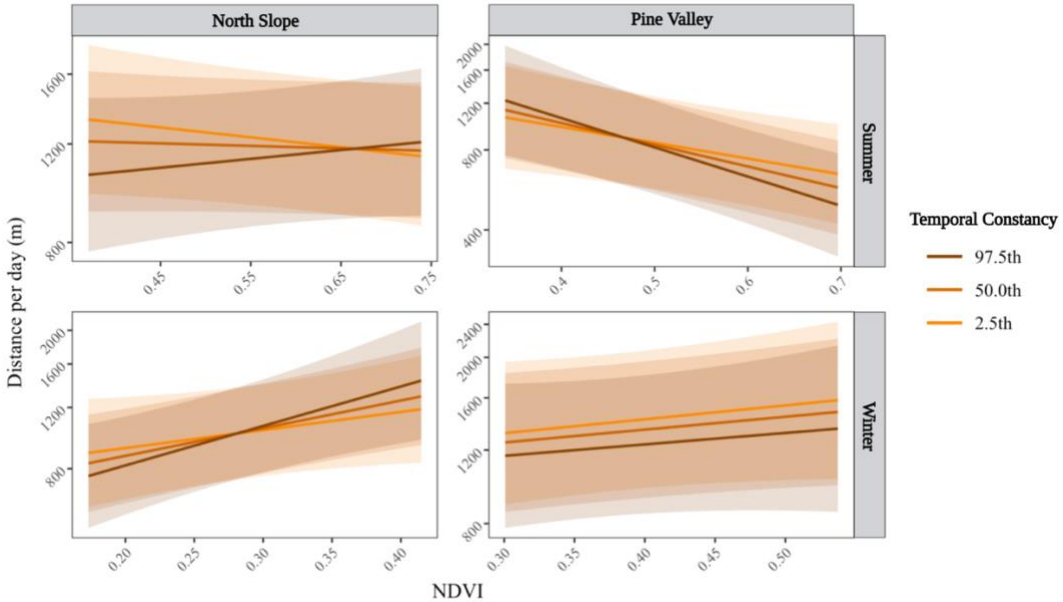
Supplementary Figure 3a Effect plots for interaction between home range area and spatial constancy.



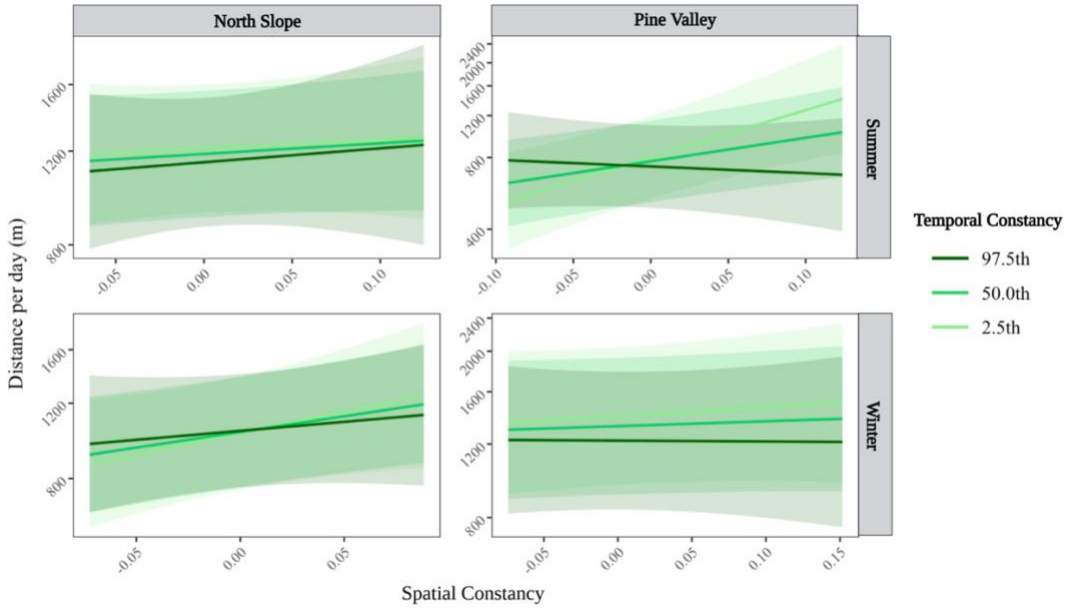
Supplementary Figure 3b Effect plots for interaction between home range area and temporal constancy.



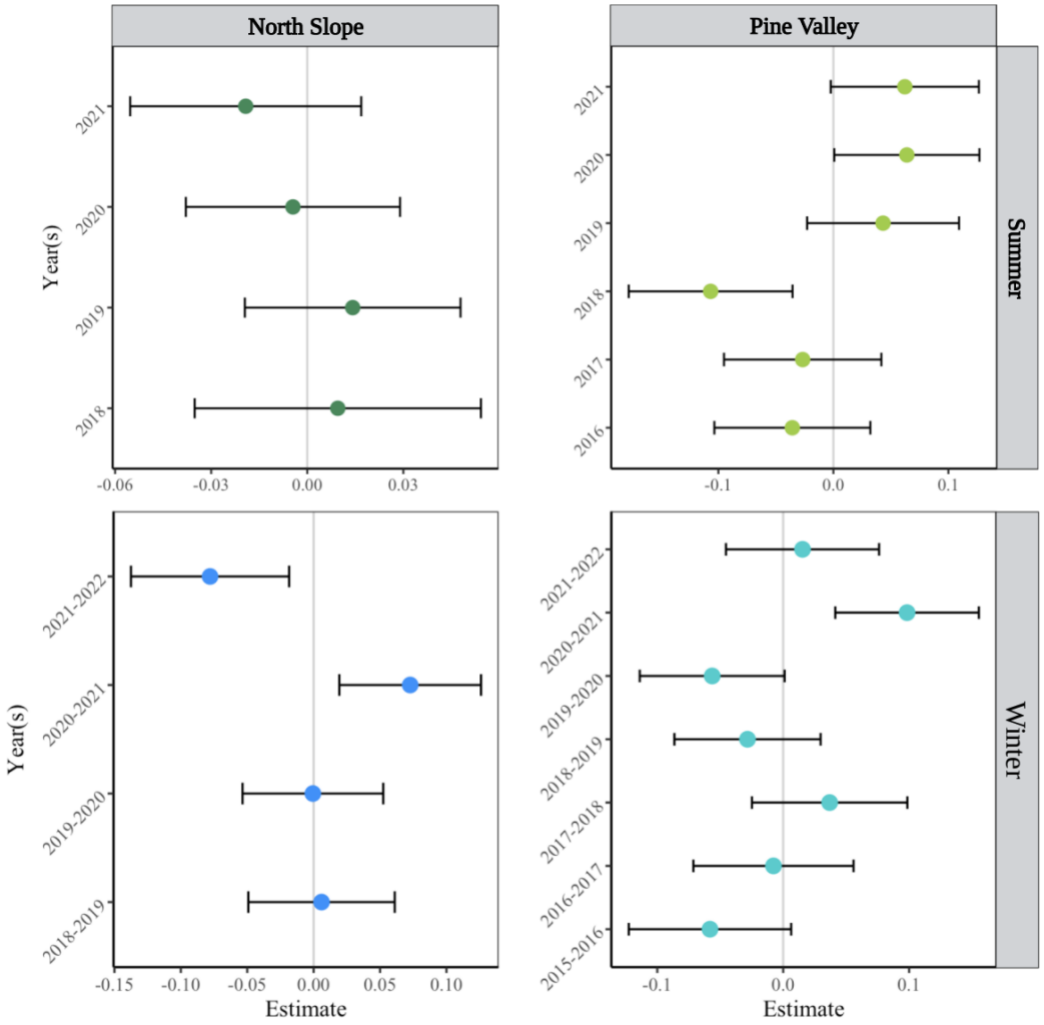
Supplementary Figure 3c Effect plots for interaction between forage availability (mean NDVI) and spatial constancy.



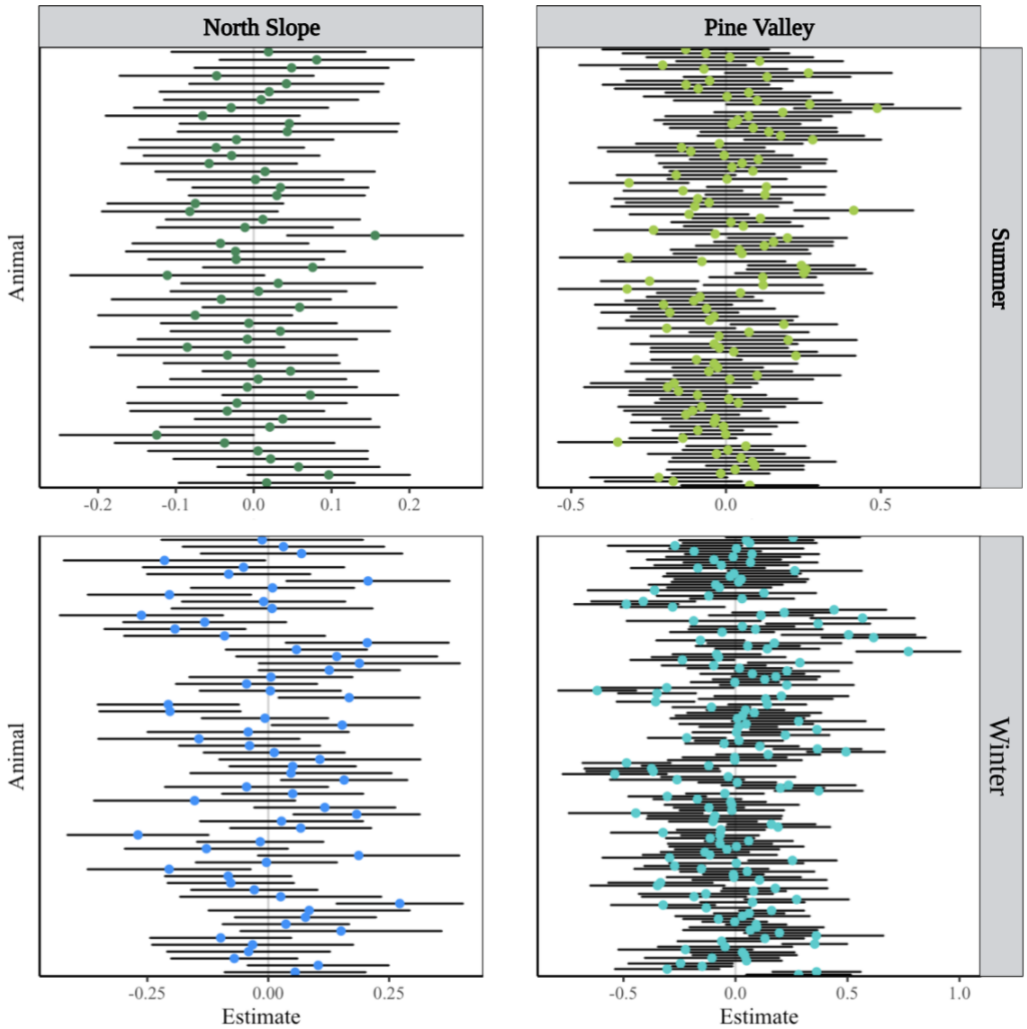
Supplementary Figure 3d Effect plots for interaction between forage availability (mean NDVI) and temporal constancy.



Supplementary Figure 3e Effect plots for interaction between spatial constancy and temporal constancy.



Supplementary Figure 4 Effect plot for random effects of year used in linear mixed models. Point represents mean effect and black bars denote the 95% confidence interval.



Supplementary Figure 5 Effect plot for random effects of animal ID used in linear mixed models. Point represents mean effect and black bars denote the 95% confidence interval.